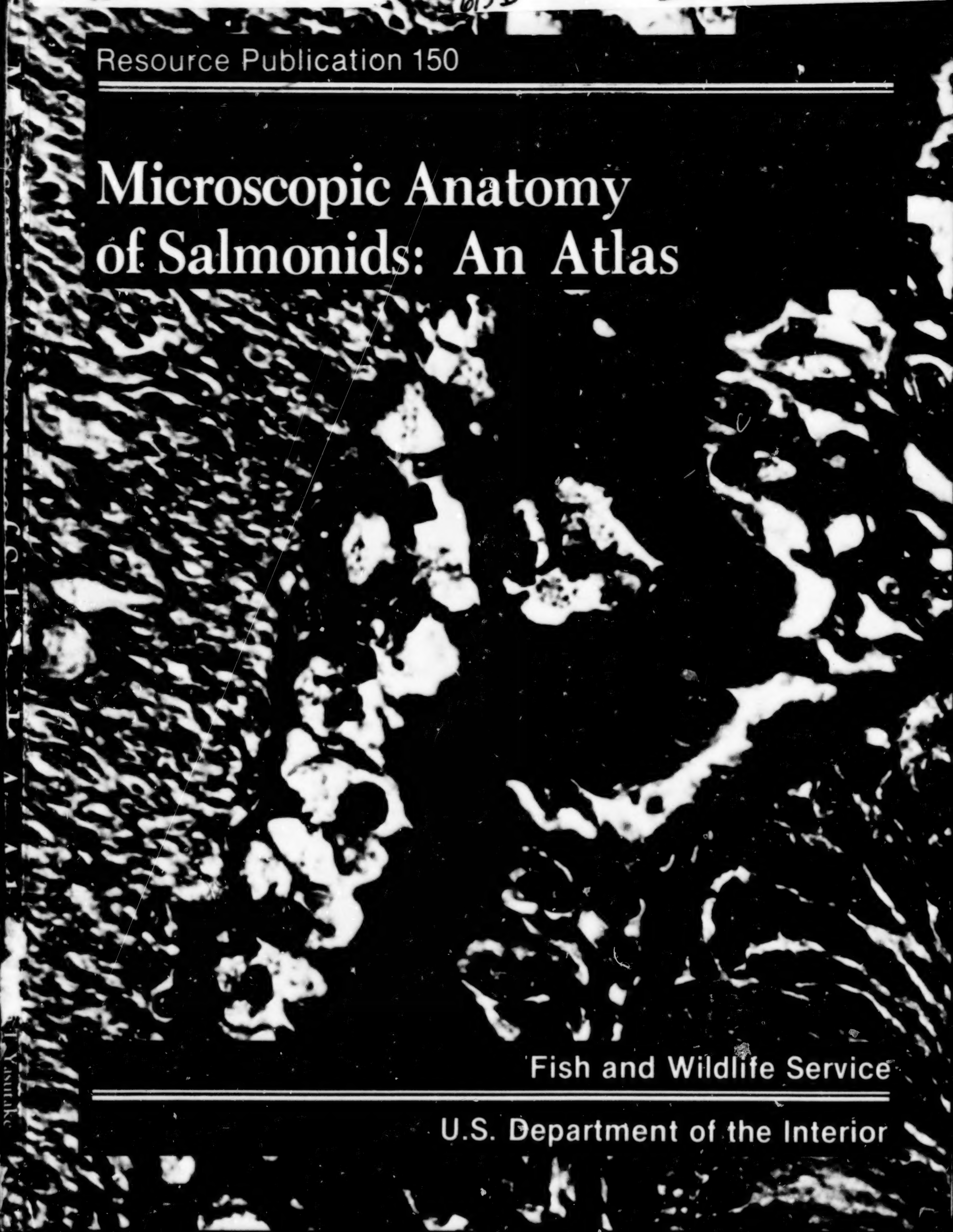
SEP 29 1983
613-B
I 49.66:150

Resource Publication 150

Microscopic Anatomy of Salmonids: An Atlas



Fish and Wildlife Service

U.S. Department of the Interior

RESOURCE PUBLICATIONS

This publication of the Fish and Wildlife Service is a miscellaneous series for separately issued popular or instructional materials dealing with investigations related to wildlife and sport fish. Each is published as a separate paper. The Service distributes a limited number of these reports for the use of Federal and State agencies and cooperators. A list of recent issues appears on inside back cover.

As the Nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural resources. This includes fostering the wisest use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for the enjoyment of life through outdoor recreation. The Department assesses our energy and mineral resources and works to assure that their development is in the best interests of all our people. The Department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.

March 3, 1849

Library of Congress Cataloging in Publication Data

Yasutake, William T.
Microscopic anatomy of salmonids.

(Resource publication / United States Dept. of the Interior, Fish and Wildlife Service ; no. 150)
Includes bibliographies and index.
Supt. of Docs. no.: I 49.66:150
1. Rainbow trout—Anatomy—Atlases. 2. Salmonidae—Anatomy—Atlases. 3. Histology—Atlases. 4. Fishes—Anatomy—Atlases. I. Wales, Joseph H. II. Title.
III. Series: Resource publication (U.S. Fish and Wildlife Service) ; no. 150.
S914.A3 no. 150 333.95'40973s [597'.55] 82-600365
[QL638.S2]

NOTE: Use of trade names does not imply U.S. Government endorsement of commercial products.

A

Microscopic Anatomy of Salmonids: An Atlas

William T. Yasutake

U.S. Fish and Wildlife Service
Seattle National Fishery Research Center
Seattle, Washington

Joseph H. Wales

Department of Food Sciences
Oregon State University
Corvallis, Oregon

UNITED STATES
DEPARTMENT OF THE INTERIOR
FISH AND WILDLIFE SERVICE
Resource Publication 150
Washington, D.C. • 1983

Contents

Page

Preface v
Acknowledgments vi
- **I. Introduction** 1
    - References 1
- **II. Supportive Tissues** 7
    - Cartilage 7
    - Bone 7
    - Notochord 7
    - Muscle 7
    - References 8
- **III. Skin and Scales,** by Joyce W. Hawkes 14
    - Skin 14
    - Scales and Pigment Cells 14
    - References 15
- **IV. Digestive System** 24
    - Oral Cavity 24
    - Esophagus 25
    - Stomach 25
    - Intestine 25
    - Pyloric Caeca 25
    - Rectum 25
    - Liver 25
    - Biliary Tissue 26
    - Pancreas 26
    - Swim Bladder (Gas Bladder) 27
    - References 27
- **V. Respiratory System** 62
    - References 63
- **VI. Cardiovascular System** 70
    - Heart 70
    - Arteries and Veins 71
    - Lymphatic System 71
    - References 71
- **VII. Blood** 82
    - Erythrocytes 82
    - Lymphocytes 82
    - Neutrophils (Polymorphonuclear Leukocytes) 82
    - Thrombocytes 83
    - Monocytes and Macrophages 83
    - References 83

VIII. Hematopoietic Tissues 91
Hematopoietic Kidney 91
Spleen 91
Thymus Gland 91
References 91
IX. Urinary System, by J. D. Hendricks 97
References 98
X. Nervous System 104
Brain 104
Spinal Cord 105
Neurosecretory System 105
References 105
XI. Special Sensory Organs and Tissues 117
Optic Tissue 117
Olfactory Tissue 117
Gustatory Tissue 117
Lateral Line Tissue 118
Auditory Tissue 118
Pineal Organ 118
Rodlet Cells 119
References 119
XII. Reproductive System 145
Testis 145
Ovary 145
References 145
XIII. Endocrine System 152
Pituitary Gland (Hypophysis) 152
Thyroid Gland 153
Corpuscles of Stannius 154
Saccus Vasculosus 154
Ultimobranchial Gland 154
References 154
APPENDIX: Fixation and Staining Procedures 180
INDEX 185

List of Plates

Page
1. Head of Rainbow Trout 3
2. Tissues of Head 5
3. Internal Anatomy of Rainbow Trout (color) 6
4. Cartilage and Bone 11
5. Muscle 13
6. Skin 19
7. Skin and Scales 21
8. Pigment Cells 23
9. Digestive Tract 33
10. Teeth 35
11. Esophagus 37
12. Cardiac Stomach 39

13. Pyloric Stomach (1) 41
14. Pyloric Stomach (2) (color) 43
15. Pyloric Caeca 45
16. Ascending Intestine (1) 47
17. Ascending Intestine (2) (color) 49
18. Descending Intestine 51
19. Liver 53
20. Biliary Tissue 55
21. Pancreatic Tissue 57
22. Pancreas and Islet of Langerhans (color) 59
23. Swim Bladder 61
24. Gills 67
25. Pseudobranch 69
26. Circulatory System 74
27. Heart (1) 75
28. Heart (2) 77
29. Arteries and Veins 79
30. Lymphatic System 81
31. Blood (1) (color) 87
32. Blood (2) (color) 89
33. Spleen 93
34. Thymus 95
35. Kidney (1) 101
36. Kidney (2) 103
37. Central Nervous System 109
38. Brain 111
39. Nervous Tissue 113
40. Caudal Neurosecretory System 115
41. Optic Tissue 125
42. Retina (color) 127
43. Olfactory Tissue 129
44. Gustatory Tissue 131
45. Tactile Organs 133
46. Lateral Line Tissue 135
47. Lateral Line Tissue (color) 137
48. Auditory Tissue 139
49. Pineal Organ 141
50. Rodlet Cells 143
51. Testis 149
52. Ovary 151
53. Pituitary Gland (1) 161
54. Pituitary Gland (2) (color) 163
55. Pituitary Gland (3) (color) 165
56. Thyroid Gland 167
57. Adrenal Gland 169
58. Chromaffin Cells (color) 171
59. Corpuscle of Stannius (1) 173
60. Corpuscle of Stannius (2) (color) 175
61. Saccus Vasculosus 177
62. Ultimobranchial Gland 179

Preface

The subject of salmonid histology has received only limited treatment in most works on comparative vertebrate histology. N. Kawamoto and Y. Fukuda (1969) provided line drawings of electron micrographs of various species of fish in their "Illustrations of fish histology by electronmicroscopy (Osteichthyes)." More recently, three books on fish histology have been published: "Atlas of trout histology," by B. G. Anderson and D. L. Mitchum (1974); "Anatomy and histology of the channel catfish," by J. M. Grizzle and W. A. Rogers (1976); and "Histology of the striped bass," by D. B. Groman (1982). The book by Anderson and Mitchum serves as a general introduction to the subject, whereas the present work is intended to meet an expressed need for a detailed illustrated manual of salmonid histology. This project was begun more than 10 years ago in response to numerous inquiries about a source of information on the microscopic anatomy of salmonids, from researchers, professors, students, biologists, and others in fisheries and related fields.

The strength and value of an atlas such as this obviously lie in the quality of the photomicrographs; therefore we selected our illustrations with special care. They include 50 plates in black and white, supplemented by 12 in color, all with detailed captions. Many significant structures or areas are shown at high magnification. The text of each of the 13 chapters has been generally limited to introductory comments. Because we consider the bibliography to be an essential part of this atlas, we did not limit references to those mentioned in the text, but provided additional selected literature citations at the end of each chapter as sources of more detailed and specific information. A description of fixing and staining procedures in the appendix is followed by a subject index.

Acknowledgments

We thank Mrs. L. J. Hunter (Department of Food Sciences and Technology, Food Toxicology and Nutrition Laboratory, Oregon State University) for her skillful technical assistance in the preparation of slides; and Robert Rogers and Elwyn Obert (Photographic Services, Oregon State University) for processing of the black and white photographs. We acknowledge the technical assistance of D. E. Crouch and T. Ochiai (National Fishery Research Center).

Our thanks go to the following colleagues for reviewing early drafts of this manuscript: Dr. J. D. Hendricks (Department of Food Sciences and Technology, Oregon State University), Dr. R. L. Herman (National Fishery Research and Development Center, U.S. Fish and Wildlife Service, Wellsboro, Pennsylvania), Dr. M. L. Landolt (College of Fisheries, University of Washington), H. Wolf (Fish Pathology Laboratory, California Department of Fish and Game, Rancho Cordova), and Dr. K. Wolf (National Fish Health Research Laboratory, U.S. Fish and Wildlife Service, Kearneysville, West Virginia). We also thank Drs. R. W. Gould, G. A. Wedemeyer (National Fishery Research Center), and E. M. Wood (Western State Hospital, Steilacoom, Washington) for reviewing the final draft.

We are indebted to Dr. A. C. Fox (National Fishery Research Center), Professor R. O. Sinnhuber (Department of Food Sciences and Technology, Oregon State University), and Dr. R. L. Herman, for their encouragement and patience. For their guidance and support, we owe a debt of gratitude to all of the staff of the National Fishery Research Center and the Food Toxicology and Nutrition Laboratory, including the former directors of the Center (then the Western Fish Disease Laboratory), T. J. Parisot and Dr. R. R. Rucker.

We thank M. L. Hadra for her technical assistance in the preparation of the manuscript. Finally, our deepest gratitude goes to our families, particularly our wives, Fumi Yasutake and Brenda Wales, whose support made it possible to complete this project.

BLANK PAGE

Chapter I

Introduction

Histology and histopathology play important roles in the fields of human and animal medicine. Their use in fishery research and diagnosis, although not new, has not been extensive. The emerging interest in this use during the last 10–15 years was evidenced by an international symposium on the pathology of fishes, held in Washington, D.C., in 1972. The publication resulting from that meeting, "The pathology of fishes" (Ribelin and Migaki 1975), was notable in that most of the papers concerned some aspect of fish histopathology.

The rainbow trout (*Salmo gairdneri*) is used in this book primarily because the authors are most familiar with this species. It was originally found in the drainage waters of the Pacific coast of North America, and was distributed by man to all suitable waters of eastern North America and to most of the suitable waters of all the continents of the world except Antarctica (MacCrimmon 1971). The rainbow trout is used as an experimental animal by an increasing number of laboratories (Hendricks et al. 1980). Because it is domesticated, it is usually obtainable at any time of the year. It is one of the major fish species, especially in the United States, used in studies of toxicity, nutrition, the environment, disease, and genetics. The species is propagated and reared by a number of governmental agencies for sport fishing and by many commercial trout farmers for marketing.

A salmonid fingerling is an ideal animal for the application of histological techniques. We have found that there is little difference in the basic histological characteristics of salmonids of different species. The amount of calcium in the bones is less in salmonids than in most other families of teleost fishes. Bouin's fluid is our choice of fixative for routine histological examination because its components, acetic and picric acids, decalcify bone adequately to minimize sectioning problems, particularly when sagittal sections of whole small fingerlings are cut. When desired, this type of section gives the histologist or pathologist the added advantage of viewing the whole animal on a slide. It is readily apparent that there are general similarities among most animals in fundamental cytological morphology (Plates 1, 2). General mid-saggittal anatomical features are shown in Plate 3. Tissues fixed with Bouin's fluid also seem to stain more vividly with routine histological stains such as hematoxylin and eosin. The fixation procedure for routine histological examination used in most of the tissues included in this text is outlined in the Appendix. The importance of proper tissue preparation before histological analyses cannot be overstressed (Bucke 1972).

Most of the photographs in this book were made from tissues fixed in Bouin's fluid, embedded in paraffin, and stained with hematoxylin and eosin. A few of the illustrations are of materials fixed in Bouin-Hollande fluid and stained with Masson's trichrome. Blood smears and kidney imprints were stained with Leishman-Giemsa and peroxidase (technique described in Appendix).

The bibliographies for Chapters VI, VII, and VIII, "Cardiovascular System," "Blood," and "Hematopoietic Tissues," do not include many of the references listed in "Fish haematology – A bibliography," by Hawkins and Mawdesley-Thomas (1972).

All of the plates, with the exception of two scanning electron micrographs are light micrographs. Unless otherwise indicated, the black and white photomicrographs were taken by J. H. Wales and the color photomicrographs by W. T. Yasutake.

References

Anderson, B. G., and D. L. Mitchum. 1974. Atlas of trout histology. Wyoming Game Fish Dep., Bull. 13. 110 pp.

Andrew, W. 1959. Textbook of comparative histology. Oxford University Press, New York. 652 pp.

Andrew, W., and C. P. Hickman. 1974. Histology of the vertebrates. The C. V. Mosby Co., St. Louis. 439 pp.

Ashley, L. M. 1975. Comparative fish histology. Pages 3–30 *in* W. E. Ribelin and G. Migaki, eds. The pathology of fishes. University of Wisconsin Press, Madison.

Bentley, P. J. 1976. Comparative vertebrate endocrinology. Cambridge University Press, New York. 415 pp.

Bergman, R. A., and A. K. Afifi. 1974. Atlas of microscopic anatomy. W. B. Saunders Co., Philadelphia. 426 pp.

Berry, P. Y., and M. P. Low. 1970. Comparative studies on some aspects of the morphology and histology of *Ctenopharyngodon idellus*, *Aristichthys nobilis*, and their hybrid (Cyprinidae). Copeia 1970: 708–726.

Bloom, W., and D. W. Faucett. 1975. Textbook of histology, 10th ed. W. B. Saunders Co., Philadelphia. 1033 pp.

Brown, M. E., editor. 1957*a*. The physiology of fishes, vol. 1. Academic Press, New York. 447 pp.

Brown, M. E., editor. 1957*b*. The physiology of fishes, vol. 2. Academic Press, New York. 526 pp.

Bucke, D. 1972. Some histological techniques applicable to fish tissues. Pages 153–189 *in* L. E. Mawdesley-Thomas, ed. Diseases of fish. Symp. Zool. Soc. Lond. No. 30. Academic Press, New York.

Colgrove, G. S. 1966. Histological and hematological changes accompanying sexual maturation of sockeye salmon *Oncorhynchus nerka* in the Fraser River system. Int. Pac. Salmon Fish. Comm. Bull. 20: 1–28.

Corset, J. 1960. Atlas d'histologie animale. N. Boubee, Paris. 192 pp.

Dickson, D. H. 1970. The fine structure of trout blastoderm. J. Morphol. 130: 367–383.

Ehrlich, K. F., J. H. S. Blaxter, and R. Pemberton. 1976. Morphological and histological changes during the growth and starvation of herring and plaice larvae. Mar. Biol. (Berl.) 35: 105–118.

Ghittino, P. 1969. Some brief notes on anatomy and physiology of fishes. Pages 9–38 *in* Piscicoltura e Ittiopathologia, Vol. I Piscicoltura. Edizione Rivista di Zootecnia, Italy.

Goodrich, E. S. 1958. Studies on the structure and development of vertebrates. Dover Publications, New York. 2 vols.

Grizzle, J. M., and W. A. Rogers. 1976. Anatomy and histology of the channel catfish. Auburn University Agricultural Experiment Station, Auburn, Alabama. 94 pp.

Groman, D. B. 1982. Histology of striped bass. Am. Fish. Soc. Monogr. No. 3. 120 pp.

Ham, A. W., and D. H. Cormack. 1979. Histology, 8th ed. J. B. Lippincott Co., Philadelphia. 966 pp.

Harder, W. 1975. Anatomy of fishes. E. Schweizerbart'sche Verlagsbuchhandlung (Nagele u. Obermiller) Stuttgart. Part I. Text 612 pp. Part II: Figures and Plates 132 pp. (Transl. from German)

Hawkins, R., and L. E. Mawdesley-Thomas. 1972. Fish haematology – a bibliography. J. Fish Biol. 4: 193–232.

Hendricks, J. D., J. H. Wales, R. O. Sinnhuber, J. E. Nixon, P. M. Loveland, and R. A. Scanlan. 1980. Rainbow trout (*Salmo gairdneri*) embryos: a sensitive animal model for experimental carcinogenesis. Fed. Proc. 39: 3222–3229.

Holmgren, N. 1943. Studies on the head of fishes. An embryological, morphological and phylogenetical study. Part IV. General morphology of the head in fish. Acta Zool. (Stockh.) 24: 1–188.

Kawamoto, N., and Y. Fukuda. 1969. Illustrations of fish histology by electronmicroscopy (Osteichthyes). Ishizaki-Shoten, Tokyo, Japan. 151 pp.

Kendall, J. I. 1940. The microscopic anatomy of vertebrates. Lea and Febiger, Philadelphia. 342 pp.

Kingsley, J. S. 1926. Outlines of comparative anatomy of vertebrates, 3rd ed. P. Blakiston Sons & Co., Philadelphia. 470 pp.

Knight, A. E. 1963. The embryonic and larval development of the rainbow trout. Trans. Am. Fish. Soc. 92: 344–355.

Lagler, K. F., J. E. Bardach, P. R. Miller, and D. R. M. Passino. 1977. Ichthyology, 2nd ed. John Wiley & Sons, Inc., New York. 545 pp.

Leake, L. D. 1975. Comparative histology. Academic Press, New York. 740 pp.

Leeson, F. S., and C. R. Leeson. 1979. A brief atlas of histology. W. B. Saunders Co., Philadelphia. 276 pp.

MacCrimmon, H. R. 1971. World distribution of rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 28: 663–704.

Mahon, E. F., and W. S. Hoar. 1956. The early development of the chum salmon, *Oncorhynchus keta* (Walbaum). J. Morphol. 98: 1–48.

Meyer, V., and G. Knorr, editors. 1977. Atlas zur Anatomie und Morphologie der Nutzfische [Atlas of anatomy and morphology of commercial fish]. Verlag Paul Parey, Berlin. 15 pp.

Patt, D. I., and G. R. Patt. 1969. Comparative vertebrate histology. Harper & Row, New York. 438 pp.

Ribelin, W. E., and G. Migaki, editors. 1975. The pathology of fishes. University Wisconsin Press, Madison. 1004 pp.

Riddle, M. C. 1917. Early development of the chinook salmon. Puget Sound Mar. Stn. Publ. 1: 319–338.

Roberts, R. J., editor. 1978. Fish pathology. Bailliere Tendall, London. 318 pp.

Robertson, O. H., and B. C. Wexler. 1960. Histological changes in the organs and tissues of migrating and spawning Pacific salmon *Oncorhynchus*. Endocrinology 66: 222–239.

Sheehan, D. C., and B. B. Hrapchak. 1980. Theory and practice of histotechnology. C. V. Mosby Co., St. Louis. 481 pp.

Shimomura, M. 1969. Histological changes of various organs in the fry of chum salmon and of rainbow trout during the seaward migration or following the experimental transference into sea water from fresh water. Bull. Jpn. Soc. Sci. Fish. 35: 273–283.

Tamura, E., and Y. Honma. 1972. Histological observations on another dealfish, *Trachipterus ishikawai*, caught off the coast of Sado Island in the Japan Sea. Annu. Rep. Sado Mar. Biol. Stn., Nigata Univ. 62: 9–22.

Wedemeyer, G. A., and W. T. Yasutake. 1977. Clinical methods for the assessment of the effects of environmental stress on fish health. U.S. Fish Wildl. Serv., Tech. Pap. 89. 18 pp.

Wood, E. M., W. T. Yasutake, J. E. Halver, and A. N. Woodall. 1960. Chemical and histological studies of wild and hatchery salmon in fresh water. Trans. Am. Fish. Soc. 89: 301–307.

Wood, E. M., W. T. Yasutake, A. N. Woodall, and J. E. Halver. 1957. The nutrition of salmonid fishes. I. Chemical and histological studies of wild and domestic fish. J. Nutr. 61: 465–478.

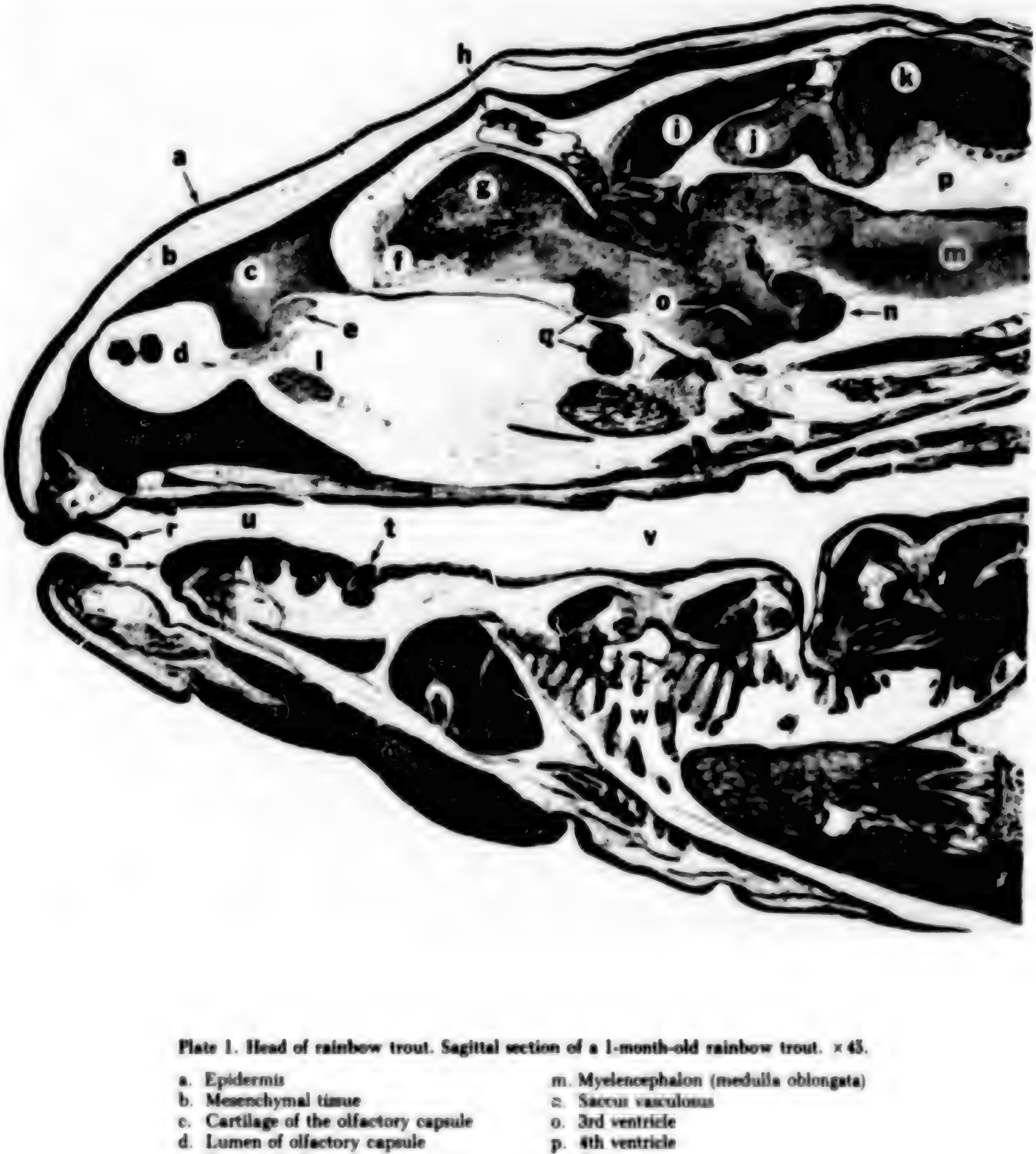
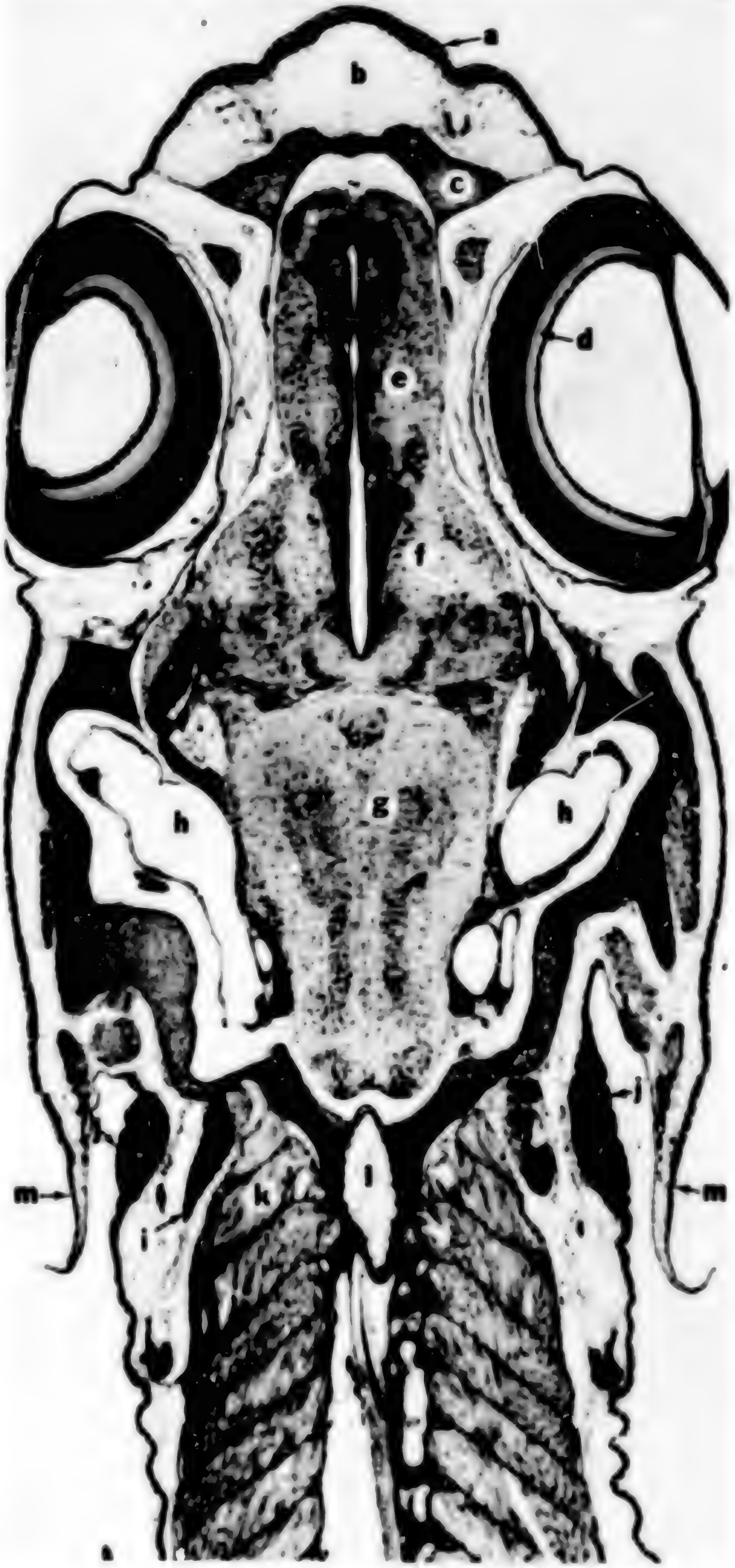


Plate 1. Head of rainbow trout. Sagittal section of a 1-month-old rainbow trout. ×45.

a. Epidermis
b. Mesenchymal tissue
c. Cartilage of the olfactory capsule
d. Lumen of olfactory capsule
e. Portion of olfactory nerve
f. Olfactory lobe
g. Telencephalon (forebrain)
h. Pineal organ
i. Mesencephalon (optic lobe)
j. Cerebellar valvula
k. Metencephalon (cerebellum)
l. Diencephalon (between brain)
m. Myelencephalon (medulla oblongata)
n. Saccus vasculosus
o. 3rd ventricle
p. 4th ventricle
q. Optic nerves
r. Oral valve
s. Tongue
t. Tooth
u. Oral region
v. Pharyngeal region
w. Gills

Plate 2. Tissues of head. Frontal section through the head of a 1-month-old rainbow trout. ×50.

a. Epidermis
b. Mesenchyme
c. Cartilage
d. Retina
e. Telencephalon (forebrain)
f. Mesencephalon (optic lobes)
g. Metencephalon (cerebellum)
h. Semicircular canals
i. Ganglion
j. Thymus
k. Muscle
l. Notochord
m. Operculum


a
b
c
d
e
f
g
h
h
j
m
m
k
l
i

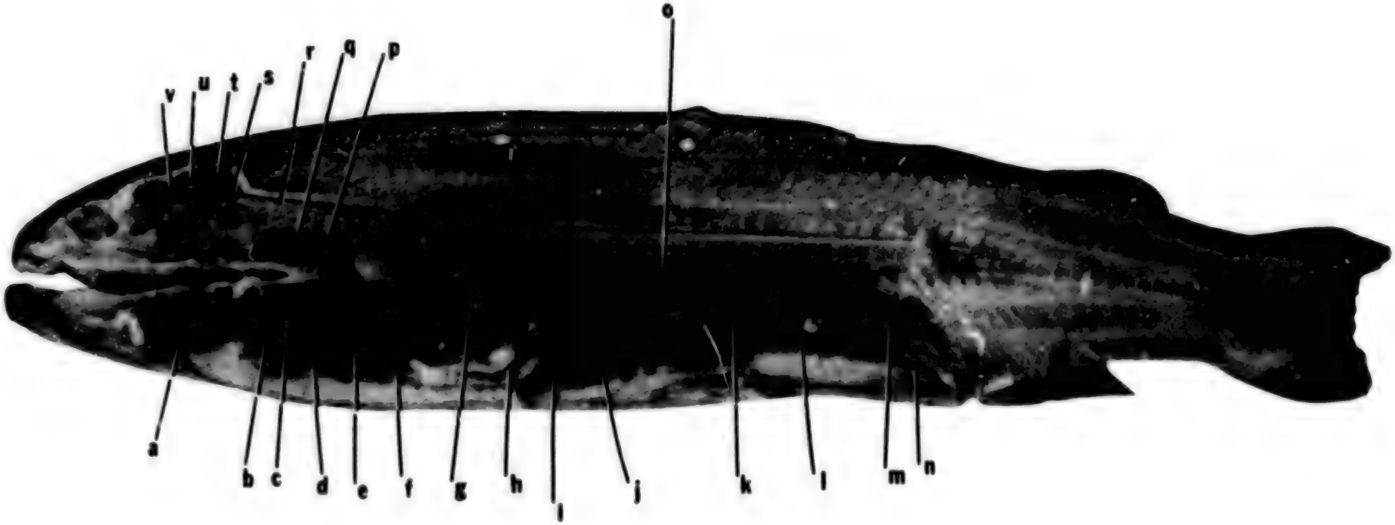


Plate 3. Internal anatomy of a 10-month-old rainbow trout. (Photo by C. L. Johnson)

a. Gills
b. Bulbus arteriosus
c. Atrium
d. Ventricle
e. Liver
f. Pyloric caeca
g. Cardiac stomach
h. Pyloric stomach
i. Spleen
j. Small intestine
k. Air bladder
l. Large intestine
m. Urinary bladder
n. Rectum
o. Kidney
p. Esophagus
q. Head (hematopoietic) kidney
r. Vertebral column
s. Medulla oblongata
t. Cerebellum
u. Optic lobe
v. Cerebral hemisphere

BLANK
PAGE

Chapter II

Supportive Tissues

Supporting and connecting tissues can be divided into three categories: fibrous connective tissue, cartilage, and bone (Harder 1975). The notochord may constitute a fourth category. The first three types of tissue consist mainly of intercellular substance, the nonliving material found between cells; in contrast, the matrix of the notochord is intracellular. The intercellular substance is fibrous and soft in the fibrous connective tissue, elastic in the cartilaginous tissue, and hard in bone. All of the supportive and connective tissues are embryologically formed from the mesoderm. Connective tissue functions chiefly to connect the three tissues of the body—epithelial, muscular, and nervous.

Fishes have more kinds of supportive tissue and more kinds of tissues intermediate between cartilage and bone than any other vertebrates (Harder 1975). In this chapter, we briefly discuss cartilage, bone, notochord, and muscle.

Cartilage

Cartilage forms the structural elements of the skeleton in embryonic and very young trout, and almost disappears in older fish. It is a specialized form of connective tissue, consisting of cells (chondrocytes) surrounded by a matrix of collagenous fibers and a ground substance known as chondroitin sulfate. Initially an aggregation of mesenchyme cells become specialized as chondrocytes. These early chondroblasts multiply to form a compact mass of cartilaginous tissue (Kendall 1940). Eventually, as the basophilic matrix accumulates around the chondrocytes, these cells become isolated in lacunae, which appear in sections as clear, more or less spherical spaces. Surrounding the cartilaginous elements is a perichondrial sheath composed of fibroblasts and collagenous fibers.

Cartilage can be roughly divided into three major types: hyaline, elastic, and fibrous. Of the three, hyaline is the most common and most typical of the cartilages (Plate 4, Fig. 4).

Bone

Histologically, fish bones are basically similar to those of higher vertebrates. Unlike mammals, however, fishes do not have any hematopoietic elements within the bone. In general, there are two types of fish bones, cellular and acellular. Cellular bone contains osteocytes and is found in lower orders, such as the Salmoniformes, which includes the trouts. Fish of higher orders, such as the Perciformes, usually have acellular bones, which are characterized by a lack of osteocytes (Moss 1961, 1963; Roberts 1978).

Bone histogenesis takes place in two forms, direct and indirect. In direct bone formation, the bone is formed in association with the dermis; in indirect bone formation, it is formed by the perichondral ossification of the hyaline cartilage (Grizzle and Rogers 1976). The osteoblasts of the periosteum do not leave cavities as they become enclosed; the spaces originally occupied by these cells are filled with a "bony" substance, largely calcium phosphate. The gill arches of trout are of cellular bone. Here the osteocytes are enclosed in the calcified intercellular substance, as in higher vertebrates (Harder 1975). The bone of fishes is vascularized by blood vessels located in strands of connective tissue.

Notochord

The superficial appearance of notochordal tissue (Plate 4, Fig. 1) is similar to that of adipose tissue. Kendall (1940) observed that the cells that form the notochord resemble fat cells because they result from the accumulation of intracytoplasmic fluid in the cells. This fluid in turn causes the vacuole to occupy almost the entire cell, thus forcing the nucleus and cytoplasm to the periphery of the cell. Cells resembling epithelial cells usually line the inner surface of the notochord. This cell layer is surrounded by an elastic membrane layer made up of fibroblasts and fibrous tissue, which are associated with formation of the vertebral column.

Muscle

Fish and other higher vertebrates have three types of muscle cells: (1) the striated, unbranched, "voluntary" musculature (Plate 5), which forms the greatest volume of tissue in the trout; (2) the cardiac musculature, also consisting of striated fibers, but which are branching and "involuntary"; and (3) the smooth unstriated, "involuntary" musculature, much of which is in the wall of the gastrointestinal tract.

The striated muscle cell of the body musculature, or the skeletal muscles, is multinucleated (Plate 5, Fig. 3). The nuclei lie just beneath the membranous sarcolemma that sheathes the cell. Each cell contains several longitudinal myofibrils, each of which comprises several myofilaments. The myofibrils can be seen by light microscopy, but myofilaments are visible only by electronmicroscopy. The striations that characterize this tissue originate from each of the parallel fibrils; the bands are in alignment and thus produce a band effect on the entire cell.

The striated muscle fibers of the heart are unlike those of the body musculature in that they are branching and anastomosing. They do not lie parallel to one another, and several planes may be seen when the heart muscle is sectioned for microscopical study. Another important difference is that the nuclei are located at regular intervals near the center of the cell, rather than just beneath the sarcolemma. Cardiac muscle cells lie end-to-end, rather than as the single, long slender units seen in the body musculature.

Smooth muscle cells are long and tapering and are not attached to one another end-to-end. They are without striations and thus are said to be "smooth." The nuclei are also long and tapering. If they have contracted, they may appear "wavy." Within the bundles, the cells of smooth muscles are parallel, but in adjacent bundles the cells may lie at right angles. Not only is smooth muscle found in the walls of all parts of the gastrointestinal tract, but also in the walls of blood vessels, especially arteries, and to a lesser extent in glands.

A conspicuous feature of the body musculature of most fish is the band or layer of red muscle lying medially just beneath the skin. The histogenesis of the "red" and "white" muscle fibers of the rainbow trout was studied by Nag (1972), who stated that these two kinds of muscles are involved in two kinds of swimming activity; the white fibers are related to short, strong bursts of motion, and the red fibers to more sustained activity. The red muscle tissue has a higher lipid content than the white tissue, and a larger number of mitochondria per cell.

References

Amprino, R., and G. Godina. 1956. Osservazioni sul nunovamento strutturale dell 'osso in pesci teleostei. Pubbl. Stn. Zool. Napoli 28: 62–71.

Boddeke, R., E. J. Slijper, and A. van der Stelt. 1959. Histological characteristics of the body musculature of fishes in connection with their mode of life. K. Ned. Ak. Wetensch. Proc. Ser. C. 62: 576–588.

Cameron, H. U. 1974. The intervertebral joint of the longnose gar, *Lepisosteus osseus*. Can. J. Zool. 52: 803–804.

Eastman, J. T. 1971. The pharyngeal bone musculature of the carp, *Cyprinus carpio*. J. Morphol. 134: 131–140.

George, J. C. 1962. A histophysiological study of the red and white muscles of the mackerel. Am. Midl. Nat. 68: 487–494.

George, J. C., and F. D. Bokadawala. 1964. Cellular organization and fat utilization in fish muscle. J. Anim. Morphol. Physiol. 11: 124–132.

Geraudie, J. 1978*a*. The fine structure of the early pelvic fin bud of the trouts *Salmo gairdneri* and *S. trutta fario*. Acta Zool. (Stockh.) 59: 85–96.

Geraudie, J. 1978*b*. Scanning electron microscope study of the developing trout pelvic fin bud. Anat. Rec. 191: 391–395.

Geraudie, J., and W. J. Landis. 1981. The fine structure of the developing pelvic fin dermal skeleton in the trout *Salmo gairdneri*. Am. J. Anat. 163: 141–156.

Greene, F. C., and C. H. Greene. 1913. The skeletal musculature of the king salmon. Bull. U.S. Bur. Fish. 33: 25–59.

Grizzle, J. M., and W. A. Rogers. 1976. Anatomy and histology of channel catfish. Auburn University Agricultural Experiment Station, Auburn, Alabama. 94 pp.

Haines, W. R. 1937. The posterior end of Meckel's cartilage and related ossifications in bony fishes. Q. J. Microsc. Sci. 80: 1–38.

Harder, W. 1975. Anatomy of fishes. E. Schweizerbart'sche Verlagsbuchhandlung (Nagele u. Obermiller) Stuttgart. Part 1. 612 pp. (Transl. from German)

Hevesy, G. 1945. Rate of renewal of the fish skeleton. Acta Physiol. Scand. 9: 234–247.

Hulbert, W. C., and T. W. Moon. 1978. A histochemical and electron microscopic examination of eel, *Anguilla rostrata* red and white muscle. J. Fish Biol. 13: 527–533.

Johnston, I. A. 1973. Biochemical and physiological studies on the swimming muscles of teleosts. Ph.D. Thesis. University of Hull, England.

Johnston, I. A., P. S. Ward, and G. Goldspink. 1975. Studies on the swimming musculature of the rainbow trout. J. Fish Biol. 7: 451–458.

Kendall, J. I. 1940. The microscopic anatomy of vertebrates, 3rd ed. Lea and Febiger, Philadelphia. 354 pp.

Kilarsky, W. 1967. The fine structure of striated muscles in teleosts. Z. Zellforsch. Mikrosk. Anat. 79: 562–580.

Kolliker, A. 1859. On the different types in the microscopic structure of the skeleton of osseous fish. Proc. R. Soc. Lond. 9: 656–688.

Lopez, E. 1970*a*. Histological study on teleost cellular bone "*Anguilla anguilla* L." I. Histologic study on teleost cellular bone. Z. Zellforsch. Mikrosk. Anat. 109: 552–565.

Lopez, E. 1970*b*. Histologic study of teleost cellular bone "*Anguilla anguilla* L." II. Effect of ablation of the corpuscles of Stannius. Z. Zellforsch. Mikrosk. Anat. 109: 566–572.

Matsuura, F., and K. Hashimoto. 1954. Chemical studies on the red muscle ('chai') of goldfishes. II. Determinations of the contents of haemoglobin, myoglobin, and cytochrome c in the muscles of fishes. Bull. Jpn. Soc. Sci. Fish. 20: 308–312.

Miller, W. A., and C. J. P. Radnor. 1973. Tooth replacement in the bowfin *Amia calva* – Holostei. J. Morphol. 140: 381–395.

Moss, M. L. 1961. Osteogenesis of acellular teleost fish bone. Am. J. Anat. 108: 99–110.

Moss, M. L. 1963. The biology of acellular bone. Ann. N. Y. Acad. Sci. 109: 337–350.

Moss, M. L. 1965. Studies of the acellular bone of teleost fish. V. Histology and mineral homeostasis of fresh-water species. Acta Anat. 60: 262–276.

Moss, M. L., and A. Posner. 1960. X-ray diffraction study of acellular teleost bone. Nature (Lond.) 188: 1037–1038.

Nag, A. C. 1972. Ultrastructure and adenosine triphosphatase activity of red and white muscle fibres of the caudal region of a fish, *Salmo gairdneri*. J. Cell Biol. 55: 42–57.

Nag, A. C., and J. R. Nursall. 1972. Histogenesis of white and red muscle fibres of trunk muscles of a fish, *Salmo gairdneri*. Cytobios 6: 227–246.

Norden, C. R. 1961. Comparative osteology of representative salmonid fishes, with particular reference to the grayling *Thymallus arcticus* and its phylogeny. J. Fish. Res. Board Can. 18: 679–791.

Ogata, T., and M. Mori. 1964. Histochemical study of oxidative enzymes in vertebrate muscles. J. Histochem. Cytochem. 12: 171–182.

Patterson, S., I. A. Johnston, and G. Goldspink. 1975. A histochemical study of the lateral muscles of five teleost species. J. Fish Biol. 7: 159–166.

Piez, K. A., and J. Gross. 1960. The amino acid composition of some fish collagens. The relation between composition and structure. J. Biol. Chem. 235: 995–998.

Proctor, C., P. R. L. Mosse, and R. C. L. Hudson. 1980. A histochemical and ultrastructural study of the development of the propulsive musculature of the brown trout, *Salmo trutta* L., in relation to its swimming behaviour. J. Fish Biol. 16: 309–329.

Roberts, R. J., editor. 1978. Fish pathology. Bailliere Tendall, London. 318 pp.

Varraes, W. 1975. Some functional aspects of ossification in the cartilaginous ceratohyale during postembryonic development in *Salmo gairdneri*-Richardson, 1836 (Teleostei: Salmonidae). Forma Functio 8: 27–32.

Weisel, G. F. 1968. The salmonid adipose fin. Copeia 1968: 626–627.

Wisniowski, P. 1960. Uber den Aufbau der Knochen des Innerskelets bei Cypriniden. Anat. Anz. 80: 161–204.

Plate 4. Cartilage and Bone

Fig. 1. Cross section of the dorsal half of the body of a 3-month-old rainbow trout. This section was made just anterior to the dorsal fin. × 50.

a. Spinal cord
b. Vertebra, showing the dense cartilaginous rim (which will become calcified), and a deeply stained inner rim or sheath, which surrounds the large, vacuolated cells of the notochord.
c. Dorsal aorta
d. Posterior cardinal vein
e. Kidney
f. Dorsal surface of air bladder
g. Dorsal aorta ligament. The distortion of the ligament in this section is an artifact.
h. Striated muscle fibers

Fig. 2. Cross section of the inferior longitudinal ligament of a 3-month-old rainbow trout. × 250.

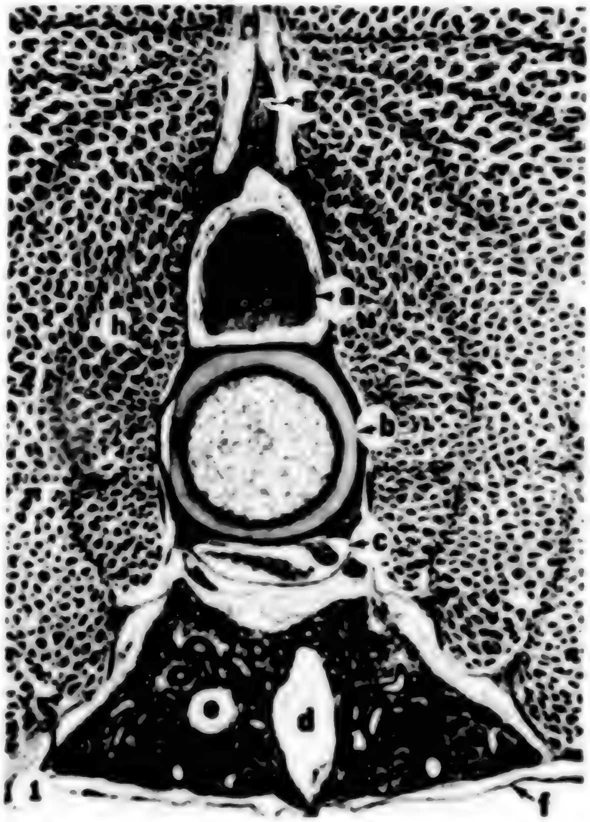
a. Chondroid-like cells
b. Sheath of connective tissue surrounding the ligament
c. Inferior longitudinal ligament composed of many bundles of collagenous fibers
d. Blood cells in aorta

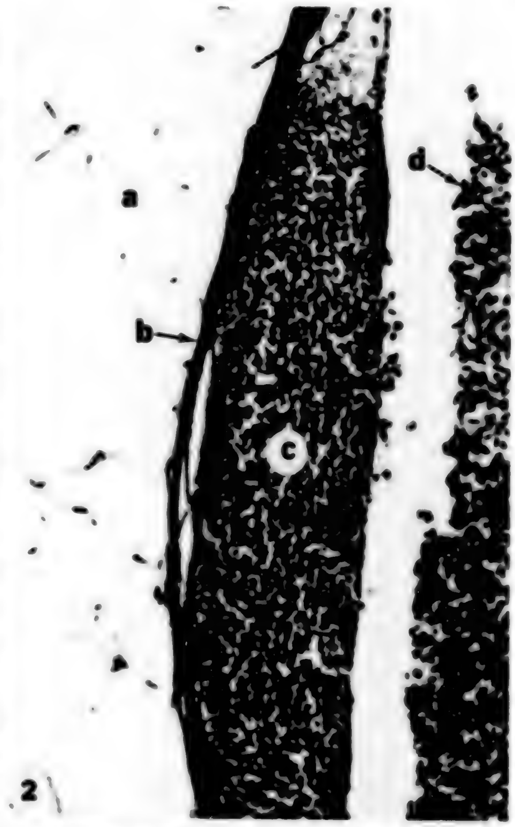
Fig. 3. Cross section of a 3-month-old trout. × 50.

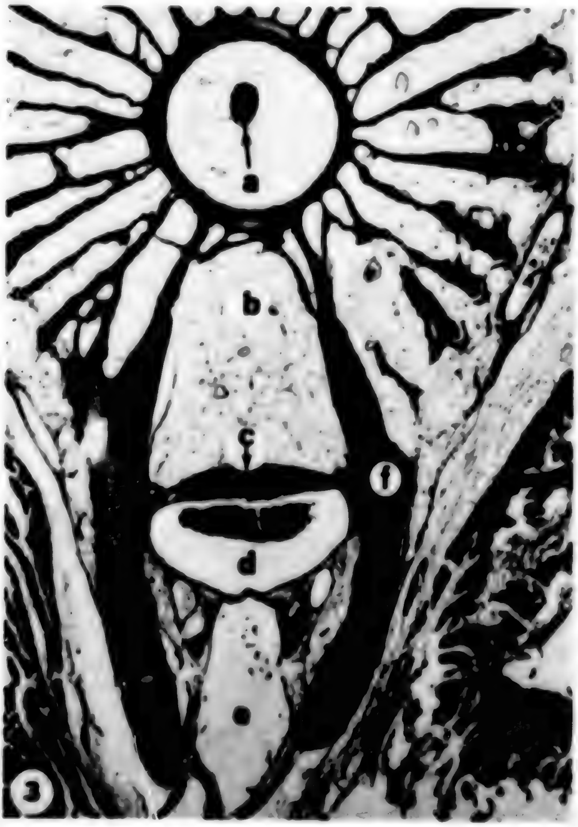
a. Notochord
b. Matrix of chrondrocytes
c. Dorsal aorta ligament
d. Median aorta containing blood cells
e. Posterior cardinal vein
f. Hemal spine

Fig. 4. Symphysis of mandibular cartilages of a 1-month-old rainbow trout, showing both hyaline and elastic types of cartilage. × 600.

a. Mitotic figure of dividing cartilage cell (hyaline)
b. Mandibular cartilage (elastic)


1


2


3

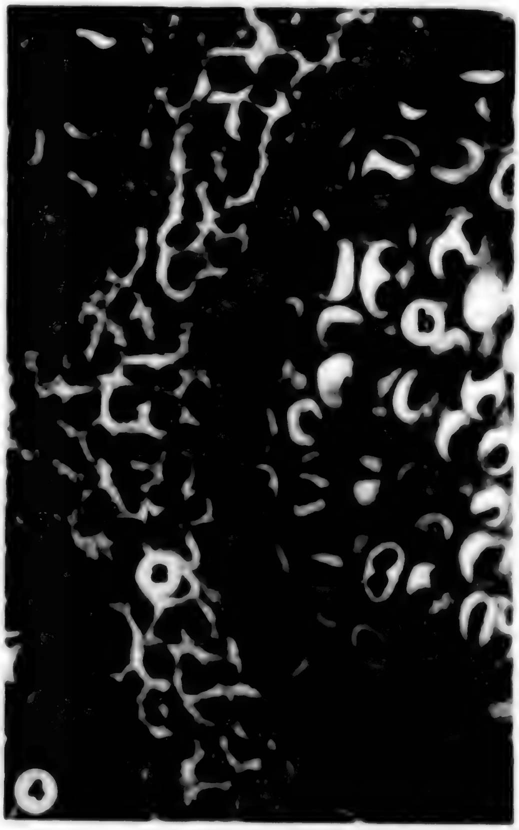

4

Plate 5. Muscle

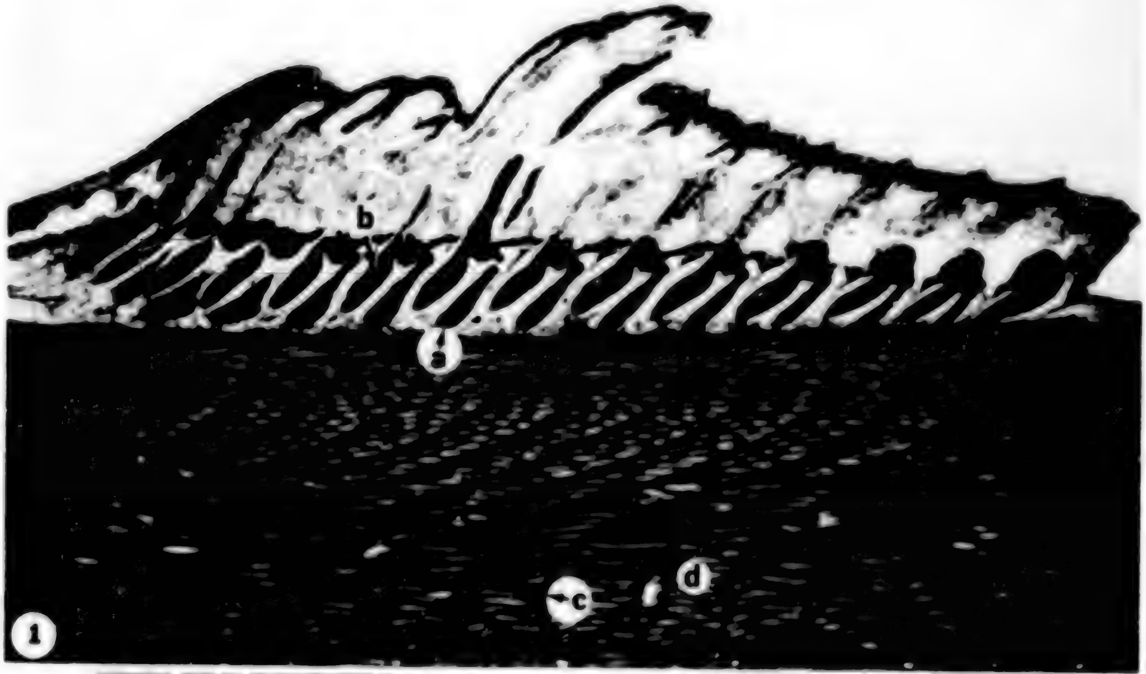
Fig. 1. Median section of the dorsal fin and musculature of a 2-month-old rainbow trout, showing the arrangement of septa between the myomeres, and the muscles of the dorsal fin rays. × 50.

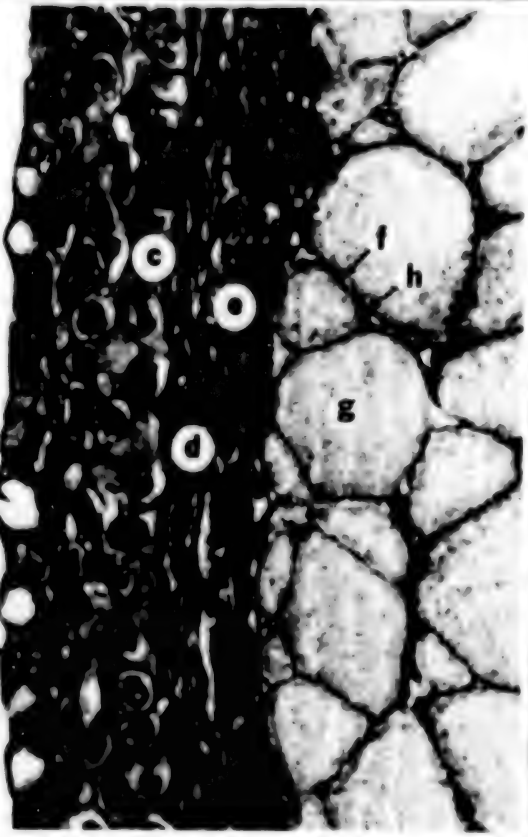
a. Erector dorsalis
b. Depressor dorsalis
c. Myosepta
d. Myomere

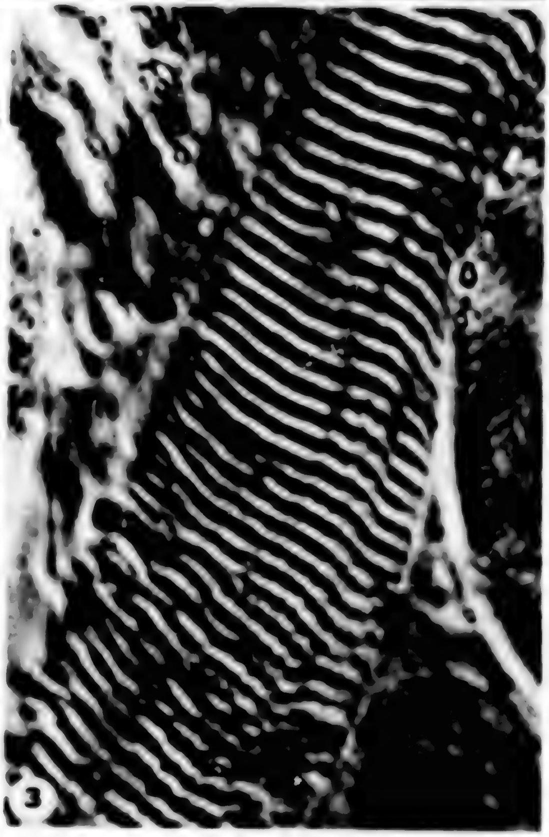
Fig. 2. Cross section of the body of a 2-month-old rainbow trout, immediately behind the head, in a scaleless area. × 500.

a. Mucous cell
b. Epidermal cell nucleus
c. Basal layer of epithelium (basement membrane lies directly beneath the epithelium)
d. Dermis
e. Fibrocyte nucleus
f. Endomysium
g. Cross section of muscle fiber
h. Muscle cell nucleus

Fig. 3. Striated muscle fiber of the dorsal musculature. Fresh tissue photographed by phase contrast. × 1400.


b
a
c
d
1


c
o
d
a
b
f
h
g
2


o
3

Chapter III

Skin and Scales

by

J. W. Hawkes
National Marine Fisheries Service
Seattle, Washington

Skin

The skin of fishes, like the skin of other vertebrates, provides protection from outside physical, chemical, and biological incursion. It is composed of two layers, the epidermis and dermis (Diagram 1; Plate 6, Fig. 1). The thickness of the epidermis of the trout varies greatly, depending on the part of the body, age, sex, maturation, and environmental stresses (Stoklosowa 1970; Harris and Hunt 1975*a*, 1975*b*; Pickering 1977). The epidermis of a yearling rainbow trout is 5 to 10 cells thick; it consists of outer squamous and cuboidal cells and a basal layer, the stratum germinativum, that gives rise to the differentiated cells outside it.

At least six types of cells have been described in the epidermis of teleosts: (1) filament-containing or Malpighian cells (Bullock and Roberts 1975; Henrickson and Matoltsy 1968*a*); (2) the mucous cells (Henrickson and Matoltsy 1968*b*; Harris et al. 1973; Pickering 1974; Harris and Hunt 1975*b*; Pickering and Macey 1977); (3) chemosensory cells (Whitear 1971); (4) club cells (Henrickson and Matoltsy 1968*c*); (5) granule cells (Roberts et al. 1971; Blackstock and Pickering 1980); and (6) chloride cells (Henrickson and Matoltsy 1968*c*; Lasker and Threadgold 1978). A filament-containing cell is the primary parenchymal cell of fish skin and contains aggregates of 75°A diameter filaments. In most species of fish, these cells do not keratinize (Downing and Novales 1971*a*, 1971*b*); consequently the outermost epidermal layers consist of living cells in contrast to the keratinized cell ghosts that make up the surface layers of the skin of other vertebrates. In a few species of fish, however, the epidermis on the protruding integumental areas is covered with a layer of keratinized cells (Mittal and Whitear 1979). In trout the outer cell membrane is a boundary between the skin and the environment, and has convoluted microridges at that boundary (Plate 6, Fig. 2). In a sense, the microridge pattern is like a "thumbprint"; it is unique for each family of fishes and may prove to be species specific. The functional significance of the microridges is not fully known, but they provide defense and assist in holding mucous secretions to the skin (Hawkes 1974*a*). Similar surface foldings, presumably performing the same function, are found on the epithelium of the gills and cornea.

Mucous cells begin differentiating in the stratum germinativum and migrate to the surface of the skin to discharge their secretions. Packets of mucus are bound by membranes and progressively fill the cell (Plate 7, Fig. 2) during the upward migration. At the skin surface, the mucous cell, a holocrine gland, pushes between the keratinocytes, discharges its entire contents, and dies (Van Oosten 1957; Brown and Wellings 1970).

The dermis, a skin zone between the epidermis and underlying muscle (Diagram 1; Plate 6, Fig. 1; Plate 7, Fig. 1), is composed of layers of elaborate arrays of connective tissue. An upper (outer) layer is the stratum spongiosum, composed of loose bands of collagen, fibroblasts, and pigment cells. Directly beneath is the stratum compactum, primarily a non-cellular layer, where a few fibroblasts intersperse between orthogonal bands of collagen. The "plywood" structure of the stratum compactum provides structural rigidity from stresses impinging on the skin and yet allows flexibility because the sheets of fibers at right angles can slip past one another during deformation.

Scales and Pigment Cells

Additional protection is provided by the scales (Plate 7, Figs. 1 and 3), which are cycloid (ovoid with smooth border) in trout and other salmonids and are considered more primitive than the ctenoid scales (with spinelike posterior ridges) of higher bony fishes. Trout scales are translucent, flexible plates that arise in the dermis (stratum spongiosum) and project at an angle into the epidermis. The outermost edge is covered with epidermis and a fold of dermal tissue.

Three kinds of pigment cells in the dermis (Plate 8, Figs. 1–4) are associated with each other to form a functional chromatophore unit (Hawkes 1974*b*). These cells are distinguished on the basis of their inclusion granules: (1) the melanophore contains melanin, which absorbs light in the entire visible range, (2) the xanthophore has drosopterin and carotenoid granules, which are yellow, and (3) the iridophores contain platelets of guanine or hypoxanthine, which reflect light, giving the fish a shiny appearance (see Bagnara and Hadley 1973, for review). The iridophores are clustered in groups of 2 to 10 cells with one to three associated melanophores. The cell body of the melanophore is below the iridophores, and the dendritic processes of the melanophores project upward and enclose the reflecting cells. The xanthophores occur at several depths through-

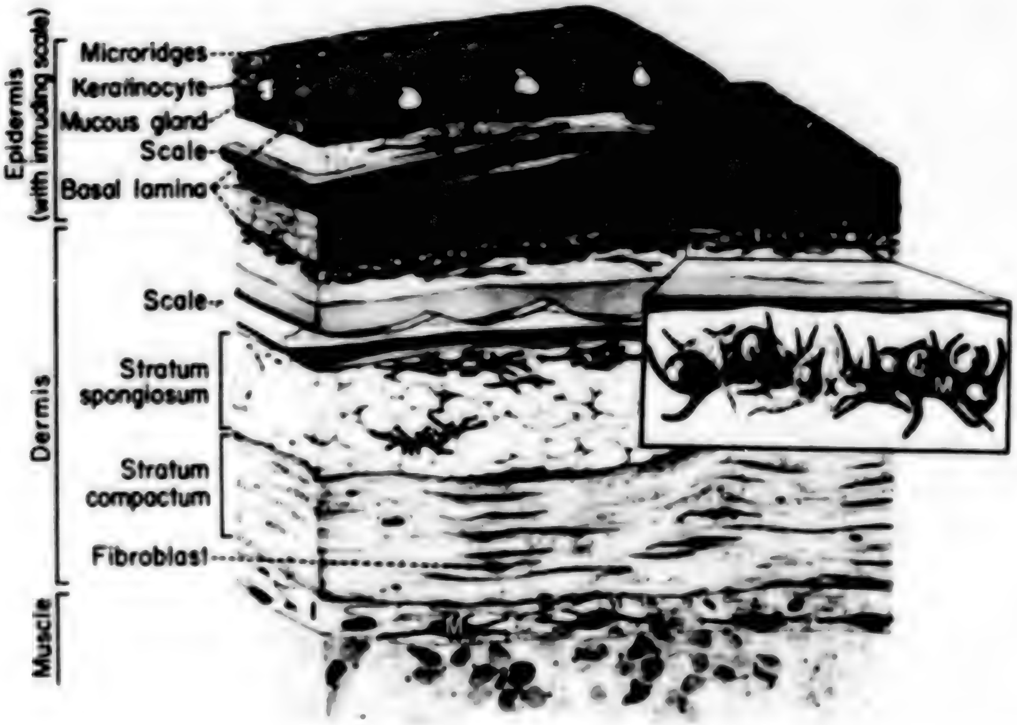


Diagram 1. Scaled skin of coho salmon (*Oncorhynchus kisutch*), showing the major skin zones and distribution of chromatophores: melanophore (m), iridophore (I), and xanthophore (X). ×75 (Adapted from Hawkes 1974a)

out the dermis, and are not closely associated with the clusters.

The chromatophores respond in concert to environmental and physiological stimuli to produce a change in color. When the fish skin appears dark, the light is absorbed by melanin in the melanophores before it reaches the iridophores. Conversely, when the skin appears light, the melanosomes are aggregated near the melanophore cell body below the iridophore and the incoming light strikes the guanine platelets and is reflected.

Beneath all these supportive and strengthening tissues, at the deepest level of the dermis, is the subcutis or hypodermis, a loose connective tissue layer. Numerous pigment cells, fat cells, small blood vessels, and nerves are present in the hypodermis, which borders the muscles beneath.

References

Abbott, F. S. 1973. Endocrine regulation of pigmentation in fish. Am. Zool. 13: 883–894.

Andrew, W. 1959. A covering called skin. Pages 96–137 *in* Textbook of comparative histology. Oxford University Press, New York.

Bagnara, J. T., and M. E. Hadley. 1973. Chromatophores and color change. Prentice-Hall, Inc., Englewood Cliffs. 202 pp.

Banerjee, T. K., and A. K. Mittal. 1975a. A cytochemical study of the "chloride cells" in the skin of a freshwater teleost *Channa striata* (Bl.) (Channidae, Pisces). Acta Histochem. 52: 126–135.

Banerjee, T. K., and A. K. Mittal. 1975b. Histochemistry and functional organization of skin of a "live-fish" *Clarias batrachus* (Linn.) (Claridae, Pisces). Mikroskopie 31: 333–349.

Bereiter-Hahn, J. 1971. Light and electron microscopic studies on function of tonofilaments in teleost epidermis. Cytobiologie 4: 73–102.

Bereiter-Hahn, J., M. Osborn, K. Weber, and M. Voth. 1979. Filament organization and formation of microridges at the surface of fish epidermis. J. Ultrastruct. Res. 69: 316–330.

Bhatia, D. 1931. On the production of annual zones in the scales of the rainbow trout *Salmo irideus*. J. Exp. Zool. 59: 45–60.

Blackstock, N., and A. D. Pickering. 1980. Acidophilic granular cells in the epidermis of the brown trout, *Salmo trutta* L. Cell Tissue Res. 210: 359–369.

Brooks, R. E., G. E. McArn, and S. R. Wellings. 1969. Ultrastructure observations on an unidentified cell type found in epidermal tumors of flounders. J. Natl. Cancer Inst. 43: 97–[illegible]

Brown, G. A., and S. R. Wellings. 1969. Collagen formation and calcification in teleost scales. Z. Zellforsch. Mikrosk. Anat. 93: 571–582.

Brown, G. A., and S. R. Wellings. 1970. Electron microscopy of the skin of the teleost *Hippoglossoides elassodon* L. Z. Zellforsch. Mikrosk. Anat. 103: 149–169.

Bullock, A. M., and R. J. Roberts. 1975. The dermatology of marine teleost fish. I. The normal integument. Oceanogr. Mar. Biol. Annu. Rev. 13: 383–411.

Bullock, A. M., R. J. Roberts, and J. D. M. Gordon. 1976. A study of the structure of the whiting integument. J. Mar. Biol. Assoc. U. K. 56: 213-226.

Burton, D. 1978. Melanophore distribution within the integumentary tissues of two teleost species, *Pseudopleuronectes americanus* and *Gasterosteus aculeatus* form *leiurus*. Can. J. Zool. 56: 526-535.

Chapman, G. B., and A. B. Dawson. 1961. Fine structure of the larval anuran epidermis, with special reference to the figures of Eberth. J. Biophys. Biochem. Cytol. 10: 425-435.

DeLamater, E. D., and W. R. Courtenay, Jr. 1974. Fish scales as seen by scanning electron microscopy. Q. J. Fla. Acad. Sci. 37: 141-149.

Downing, S. W., and R. R. Novales. 1971*a*. The fine structure of lamprey epidermis. I. Introduction and mucous cells. J. Ultrastruct. Res. 35: 282-294.

Downing, S. W., and R. R. Novales. 1971*b*. The fine structure of lamprey epidermis. II. Club cells. J. Ultrastruct. Res. 35: 295-303.

Downing, S. W., and R. R. Novales. 1971*c*. The fine structure of lamprey epidermis. III. Granular cells. J. Ultrastruct. Res. 35: 304-313.

Fishelson, L. 1972. Histology and ultrastructure of the skin of *Lepadichthys lineatus* (Gobiesocidae: Teleostei). Mar. Biol. (N. Y.) 17: 357-364.

Fishelson, L. 1973. Observations on skin structure and sloughing in the stone fish *Synanceja verrucosa* and related fish species as a functional adaptation to their mode of life. Z. Zellforsch. Mikrosk. Anat. 140: 497-508.

Fujii, R. 1968. Fine structure of the collagenous lamella underlying the epidermis of the goby, *Chasmichthys gulosus*. Annot. Zool. Jpn. 41: 95-106.

Harris, J. E., and S. Hunt. 1973. The fine structure of iridophores in the skin of the Atlantic salmon (*Salmo salar* L.). Tissue & Cell 5: 479-488.

Harris, J. E., and S. Hunt. 1975*a*. The fine structure of the epidermis of two species of salmonid fish, the Atlantic salmon (*Salmo salar* L.) and the brown trout (*Salmo trutta* L.). I. General organization and filament-containing cells. Cell Tissue Res. 157: 553-565.

Harris, J. E., and S. Hunt. 1975*b*. The fine structure of the epidermis of two species of salmonid fish, the Atlantic salmon (*Salmo salar* L.) and the brown trout (*Salmo trutta* L.). II. Mucous cells. Cell Tissue Res. 163: 535-543.

Harris, J. E., A. Watson, and S. Hunt. 1973. Histochemical analysis of mucous cells in the epidermis of brown trout (*Salmo trutta* L.). J. Fish. Biol. 5: 345-351.

Hatton, J. P., R. J. Roberts, and A. M. Bullock. 1976. The dermatology of teleost fishes – a bibliography. University of Stirling, Stirling, Scotland. 264 pp.

Hawkes, J. W. 1974*a*. The structure of fish skin. I. General organization. Cell Tissue Res. 149: 147-158.

Hawkes, J. W. 1974*b*. The structure of fish skin. II. The chromatophore unit. Cell Tissue Res. 149: 159-172.

Henrikson, R. C., and A. G. Matoltsy. 1968*a*. The fine structure of teleost epidermis. I. Introduction and filament-containing cells. J. Ultrastruct. Res. 21: 194-212.

Henrikson, R. C., and A. G. Matoltsy. 1968*b*. The fine structure of teleost epidermis. II. Mucous cells. J. Ultrastruct. Res. 21: 213-221.

Henrikson, R. C., and A. G. Matoltsy. 1968*c*. The fine structure of teleost epidermis. III. Club cells and other cell types. J. Ultrastruct. Res. 21: 222-232.

Hunter, C. R., and P. L. Nayudu. 1978. Surface folds in superficial epidermal cells of three species of teleost fish. J. Fish Biol. 12: 163-166.

Jimbo, G., T. Shibukawa, K. Kobayashi, K. Doda, and K. Kimura. 1963. Electron microscope observation on epidermis of teleost *Salmo irideus*. Bull. Yamaguchi Med. Sch. 10: 49-52.

Junqueira, L. C. U. 1973. Observations on the structure of the epidermis of teleosteans. Cienc. Cult. (Sao Paulo) 25: 1169-1174.

Junqueira, L. C. U., A. M. S. Toledo, and K. R. Porter. 1970. Observations on the structure of the skin of the teleost *Fundulus heteroclitus* (L.). Arch. Histol. Jpn. 32: 1-15.

Kamei-Takeuchi, I., and T. Kajishima. 1971. Fine structure of adult goldfish melanophores. Annot. Zool. Jpn. 44: 31-32.

Lane, E. B., and M. Whitear. 1980. Skein cells in lamprey epidermis. Can. J. Zool. 58: 450-455.

Lanzing, W. J. R., and R. S. Wright. 1974. The ultrastructure of the skin of *Tilapia mossambica* (Peters). Cell Tissue Res. 154: 251-264.

Lasker, R., and L. T. Threadgold. 1978. "Chloride cells" in the skin of the larval sardine. Exp. Cell Res. 52: 582-590.

Leonard, J. B., and R. G. Summers. 1976. The ultrastructure of the integument of the American eel, *Anguilla rostrata*. Cell Tissue Res. 171: 1-30.

Logan, V. H., and P. H. Odense. 1974. The integument of the ocean sunfish (*Mola mola* L.) (Plectognathi) with observations on the lesions from two ectoparasites, *Capsala martinierei* (Trematoda) and *Philorthagoriscus serratus* (Copepoda). Can. J. Zool. 52: 1039-1045.

Maekawa, K., and J. Yamada. 1970. Some histochemical and fine structural aspects of growing scales in the rainbow trout. Bull. Fac. Fish. Hokkaido Univ. 27: 70-78.

Maekawa, K., and J. Yamada. 1972. Morphological identification and characterization of cells involved in the growth of the goldfish scales. Jpn. J. Ichthyol. 19: 1-10.

Markert, J. R., and W. E. Vanstone. 1966. Pigments in the belly skin of coho salmon *Oncorhynchus kisutch*. J. Fish. Res. Board Can. 23: 1095-1098.

Merrilees, M. J. 1974. Epidermal fine structure of the teleost *Esox americanus* (Esocidae, Salmoniformes). J. Ultrastruct. Res. 47: 272-283.

Mittal, A. K., and T. K. Banerjee. 1975. Histochemistry and the structure of the skin of a murrel, *Channa striata* (Bloch, 1797) (Channiformes, Channidae). I. Epidermis. Can. J. Zool. 53: 833-843.

Mittal, A. K., and J. S. Munshi. 1970. Structure of the integument of a freshwater teleost, *Bagarius bagarius* (Ham.) (Sisoridae, Pisces). J. Morphol. 130: 3-10.

Mittal, A. K., and J. S. Munshi. 1971. A comparative study of the structure of the skin of certain airbreathing fresh-water teleosts. J. Zool. 163: 515-532.

Mittal, A. K., and M. Whitear. 1979. Keratinization of fish skin with special reference to the catfish *Bagarius bagarius*. Cell Tissue Res. 202: 213-230.

Mittal, A. K., M. Whitear, and S. K. Agarwal. 1980. Fine structure and histochemistry of the epidermis of the fish *Monopterus cuchia*. J. Zool. (Lond.) 191: 107-125.

Nadol, J. B., Jr., J. R. Gibbins, and K. R. Porter. 1969. A reinterpretation of the structure and development of the basement lamella: an ordered array of collagen in fish skin. Dev. Biol. 20: 304-331.

Neave, F. 1936*a*. Origin of the teleost scale-pattern and the development of the teleost scale. Nature (Lond.) 137: 1034-1035.

Neave, F. 1936*b*. The development of the scales of *Salmo*. Trans. R. Soc. Can. 5: 55-72.

Neave, F. 1940. On the histology and regeneration of the teleost scale. Q. J. Microsc. Sci. 81: 541-568.

Olson, O. P., and N. Watabe. 1980. Studies on formation and resorption of fish scales. IV. Ultrastructure of developing scales in newly hatched fry of the sheepshead minnow, *Cyprinodon variegatus* (Atheriniformes: Cyprinodontidae). Cell Tissue Res. 211: 303-316.

Onozato, H., and N. Watabe. 1979. Studies on fish scale formation and resorption. III. Fine structure and calcification of the fibrillary plates of the scales in *Carassius auratus* (Cypriniformes: Cyprinidae). Cell Tissue Res. 201: 409-422.

Pfeiffer, W., and J. Lemke. 1973. On the isolation and identification of the alarm substance from the skin of the European minnow, *Phoxinus phoxinus* (L.) (Cyprinidae, Ostariophysi, Pisces). J. Comp. Physiol. 82: 407–410.

Pickering, A. D. 1974. The distribution of mucous cells in the epidermis of the brown trout, *Salmo trutta* L. and the char, *Salvelinus alpinus* L. J. Fish Biol. 6: 111–118.

Pickering, A. D. 1977. Seasonal changes in the epidermis of the brown trout *Salmo trutta* (L.). J. Fish Biol. 10: 561–566.

Pickering, A. D., and D. J. Macey. 1977. Structure, histochemistry and the effect of handling on the mucous cells of the epidermis of the char *Salvelinus alpinus* (L.). J. Fish Biol. 10: 505–512.

Pickering, A. D., and R. H. Richards. 1980. Factors influencing the structure, function and biota of the salmonid epidermis. Proc. R. Soc. Edinb. Sect. B (Biol. Sci.) 79: 93–104.

Podoliak, H. A., and H. K. Holden, Jr. 1965. Distribution of dietary calcium to the skeleton and the skin of fingerling brown trout. Pages 64–71 in The nutrition of trout. N.Y. Conserv. Dep. Fish. Res. Bull. 28. Cortland Hatchery Report No. 33.

Roberts, R. J. 1972. Ulcerative dermal necrosis (U.D.N.) of salmon. Pages 53–88 in L. E. Mawdesley-Thomas, ed. Diseases of fish. Symp. Zool. No. 30. Academic Press, London and New York.

Roberts, R. J., M. Bell, and H. Young. 1973. Studies on the skin of plaice *Pleuronectes platessa* L. II. The development of larval plaice skin. J. Fish Biol. 5: 103–108.

Roberts, R. J., and A. M. Bullock. 1980. The skin surface ecosystem of teleost fishes. Proc. R. Soc. Edinb. Sect. B (Biol. Sci.) 79: 87–91.

Roberts, R. J., W. M. Shearer, K. G. R. Elson, and A. L. S. Munro. 1970. Studies on ulcerative dermal necrosis of salmonids. I. The skin of the normal salmon head. J. Fish Biol. 2: 223–229.

Roberts, R. J., H. Young, and J. A. Milne. 1971. Studies on the skin of plaice *Pleuronectes platessa* L. I. The structure and ultrastructure of normal skin. J. Fish Biol. 3: 87–98.

Schliwa, M. 1975. Cytoarchitecture of surface layer cells of the teleost epidermis. J. Ultrastruct. Res. 52: 377–386.

Schliwa, M., and J. Bereiter-Hahn. 1973. Pigment movements in fish melanophores: Morphological and physiological studies. III. The effects of colchicine and vinblastine. Z. Zellforsch. Mikrosk. Anat. 147: 127–148.

Schonborner, A. A., G. Boivin, and C. A. Baud. 1979. The mineralization processes in teleost fish scales. Cell Tissue Res. 202: 203–212.

Shibukawa, T. 1963. Electron microscopic observations of the skin of the teleost, *Misgurnus anguillicaudatus*. J. Yamaguchi Med. Assoc. 12: 99–103.

Stoklosowa, S. 1966. Sexual dimorphism in the skin of seatrout, *Salmo trutta*. Copeia 1966: 613–614.

Stoklosowa, S. 1970. Further observations on the sexual dimorphism in the skin of *Salmo trutta trutta* in relation to sexual maturity. Copeia 1970: 332–339.

Takeuchi, I. K., and T. Kajishima. 1971*a*. Fine structure of the melanocytes in the regenerating fins of the goldfish. Annot. Zool. Jpn. 44: 153–166.

Takeuchi, I. K., and T. Kajishima. 1971*b*. Fine structure of adult goldfish melanophores. Annot. Zool. Jpn. 44: 23–31.

Takeuchi, I. K., and T. Kajishima. 1972. Fine structure of goldfish xanthophore. J. Anat. 112: 1–10.

Terakado, K., M. Ogawa, Y. Hashimoto, and H. Matsuzaki. 1975. Ultrastructure of the thread cells in the slime gland of Japanese hagfishes, *Paramyxine atami* and *Eptatretus burgeri*. Cell Tissue Res. 159: 311–323.

Van Oosten, J. 1957. The skin and scales. Pages 207–244 in M. E. Brown, ed. The physiology of fishes, vol. 1. Academic Press, New York.

Wallin, O. 1957. On the growth, structure and developmental physiology of the scales of fishes. Inst. Freshw. Res. Drottningholm Rep. 38: 385–447.

Waterman, R. E. 1970. Fine structure of scale development in the teleost *Brachydanio rerio*. Anat. Rec. 168: 361–380.

Weisel, G. F. 1975. The integument of the paddlefish, *Polyodon spathula*. J. Morphol. 145: 143–150.

Wellings, S. R., R. G. Chuinard, and R. A. Cooper. 1967. Ultrastructural studies of normal skin and epidermal papillomas of the flathead sole, *Hippoglossoides elassodon*. Z. Zellforsch. Mikrosk. Anat. 78: 370–387.

Whitear, M. 1970. The skin surface of bony fishes. J. Zool. (Lond.) 160: 437–454.

Whitear, M. 1971. Cell specialization and sensory function in fish epidermis. J. Zool. (Lond.) 163: 237–264.

Whitear, M., A. K. Mittal, and E. B. Lane. 1980. Endothelial layers in fish skin. J. Fish Biol. 17: 43–65.

Yamada, J. 1968. A study on the structure of surface cell layers in the epidermis of some teleosts. Annot. Zool. Jpn. 41: 1–8.

Yamada, J. 1971. A fine structural aspect of the development of scales in the chum salmon fry. Jpn. Soc. Sci. Fish. 37: 18–29.

Yamada, J., and N. Watabe. 1979. Studies on fish scale formation and resorption. I. Fine structure and calcification of the scales in *Fundulus heteroclitus* (Atheriniformes: Cyprinodontidae). J. Morphol. 159: 49–66.

Zaccone, G. 1979*a*. Histochemistry of keratinization and epithelial mucins in the skin of the marine teleost *Muraena helena* (L.) (Anguilliformes, Pisces). Cell. Mol. Biol. 24: 37–50.

Zaccone, G. 1979*b*. Mucosaccharide histochemistry and histoenzymorphologic observations on the epidermis of *Ariosoma balearicum* de la Roche. Acta Histochem. 65: 191–208.

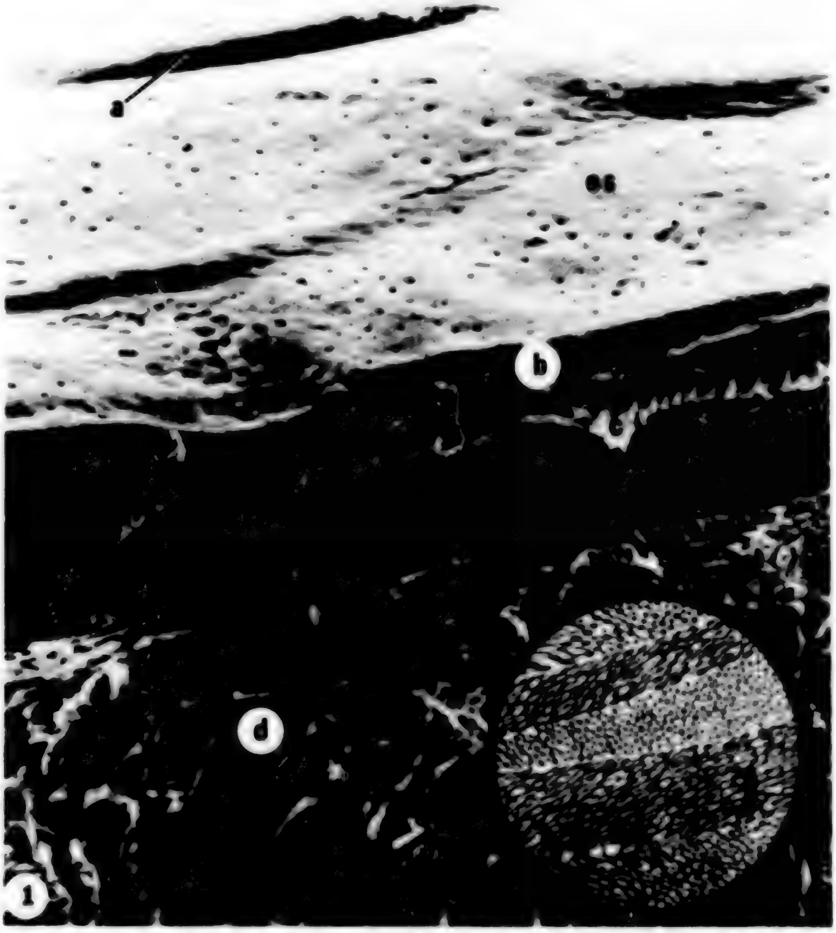
Zaccone, G. 1980. Structure and histochemistry of the epidermis in the red piranha *Serrasalmus nattereri* (Kner, 1860) (Characidae, Teleostei). Cell. Mol. Biol. 26: 75–84.

Plate 6. Skin

Fig. 1. Scanning electron micrograph of the skin of a coho salmon (*Oncorhynchus kisutch*). Part of the tissue had been trimmed in a cryostat so that both the uncut surface (OS) and a cross-sectional surface are exposed. × 200.

a. Edge of scale covered with epidermal cells
b. Sectioned edge of epidermis
c. Sectioned edge of scale
d. Sectioned edge of muscle
Inset. Magnification of the stratum compactum, showing the orthogonally arranged collagen. × 1,200.

Fig. 2. Scanning electron micrograph of the epidermal surface of a rainbow trout. Individual filament-containing cells have microridges on their surface, and their boundaries are delineated by a continuous circumferential microridge. The tops of mucous glands (arrows) squeeze between the filament-containing cells to gain access to the surface. × 2,500.


a
os
b
d
1

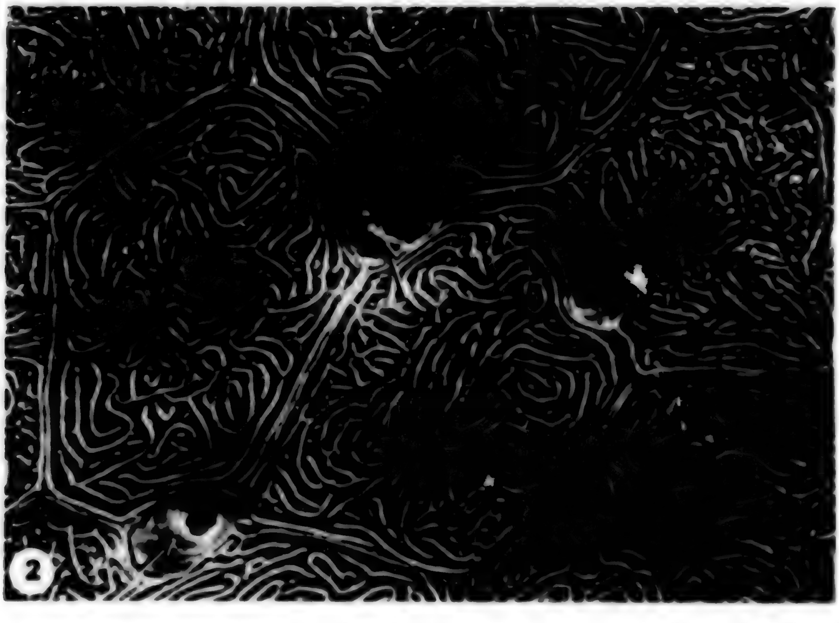

2

Plate 7. Skin and Scales

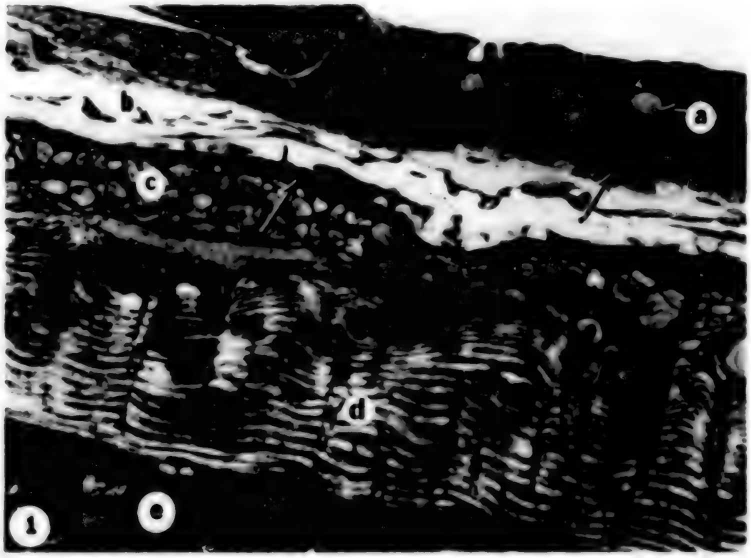
Fig. 1. Cross section of the skin from the dorsal surface of a yearling coho salmon. The mucous glands (a) are midway in their transit through the epidermis. The pigment cells (arrows) are located in several strata of the dermis. × 300.

a. Mucous cell
b. Scale
c. Stratum spongiosum
d. Stratum compactum
e. Muscle

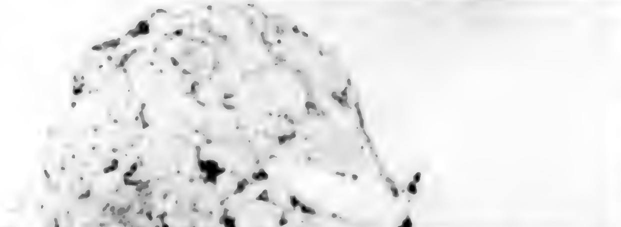
Fig. 2. Cross section of a mucous gland from an adult rainbow trout. The membrane bound packets of mucin break down as the contents of the cell are emptied. Transmission electron micrograph. × 6,400.

Fig. 3 Scale of a rainbow trout, 16 months old, reared in a hatchery at a constant temperature of 12.5° C. The annulus, which might be found on the scales of a wild trout, is absent because growth rate was uniform. Inset is the scale of a 5-month-old rainbow trout. × 40. (Photo by J. H. Wales.)

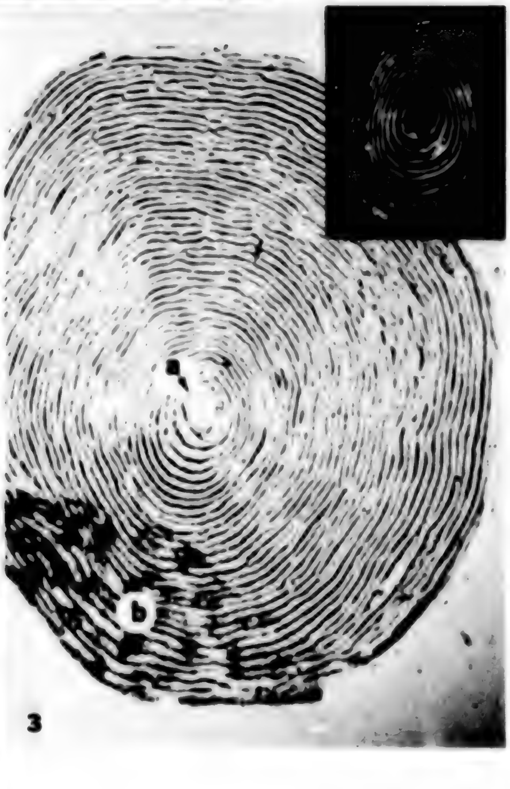
a. Point of origin (nucleus)
b. Exposed, pigmented portion. Arrow indicates one of the circuli.



1



2



3

Plate 8. Pigment Cells

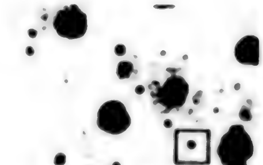
Figs. 1 and 2. Chromatophores of a living coho salmon fingerling after treatment with 0.1M KCl (Fig. 1) and 0.1M NaCl (Fig. 2). In Fig. 1 the segment granules in the melanophores (dense black) and the xanthophores (box) are aggregated. Iridophores (arrow) are associated with the melanophores. In Fig. 2 the melanosomes fill the dendritic arms of the melanophores after treatment with NaCl. × 130.

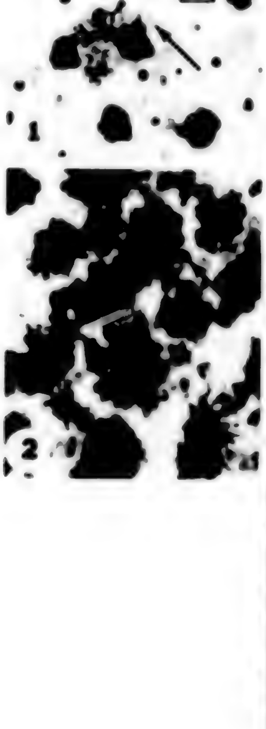
Fig. 3. Cross section of unscaled skin from the head of a coho salmon. Chromatophore unit clusters are present in the dermis in large clusters (white arrowhead) and small clusters (black arrow). × 300.

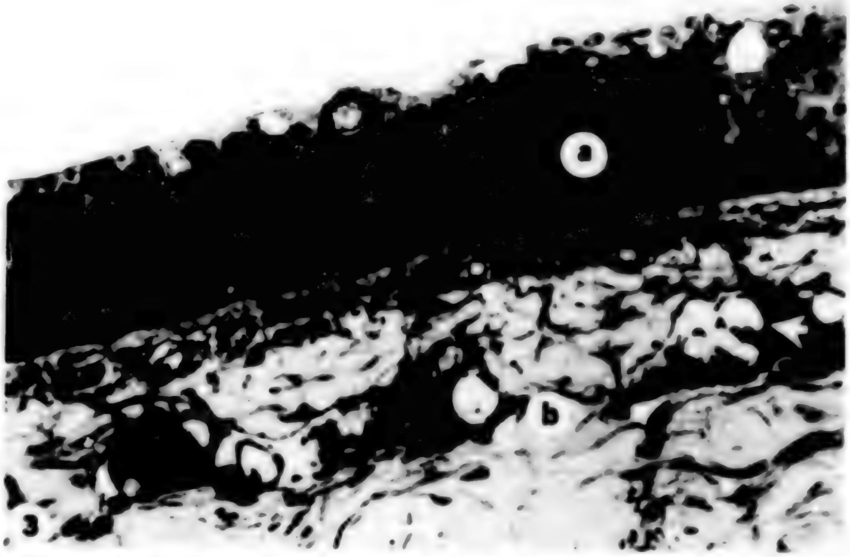
a. Epidermis
b. Dermis

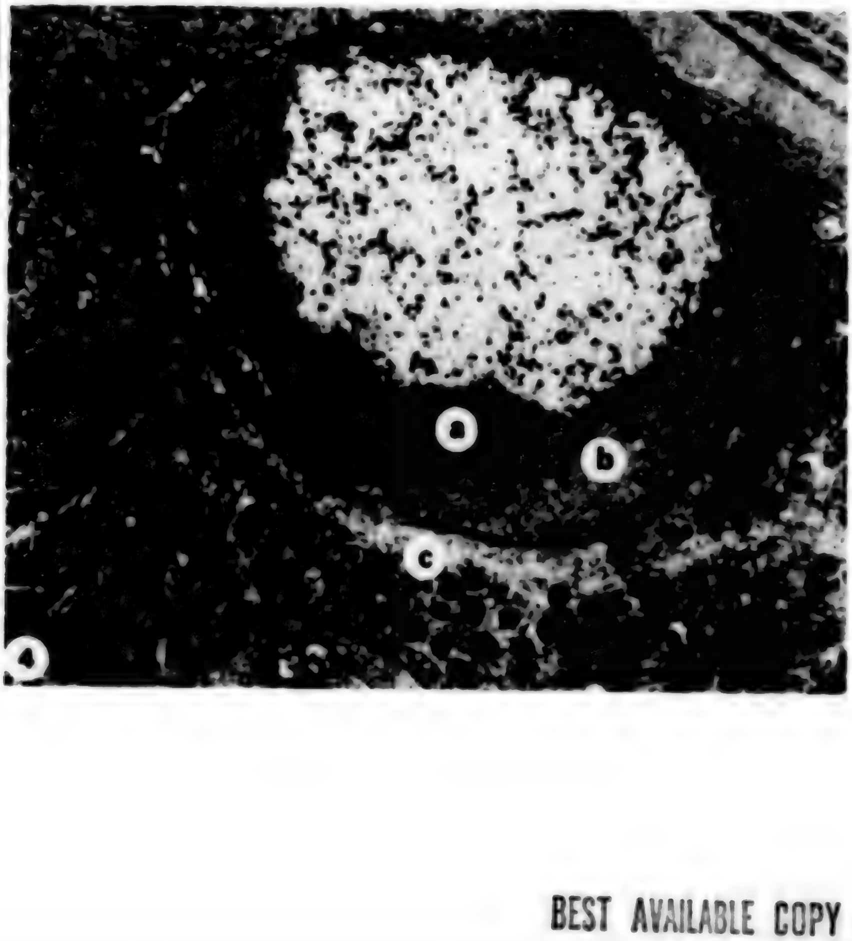
Fig. 4. Cross section of a chromatophore unit in the dorsal, scaled skin of a coho salmon. The globular iridophore typically contains clusters of mitochondria, guanine platelets, and a large nucleus. The iridophore is partly encircled by the dendritic arms of a melanophore. The melanophore is filled with dense pigment granules. × 6,500.

a. Mitochondria of the iridophore
b. Reflecting platelets of the iridophore
c. Melanophore


1


2


a
b
3


a
b
c
4

Chapter IV

Digestive System

A number of light and electronmicroscopic studies concerning various aspects of the digestive tract of fishes have been reported (Weinreb and Bilstad 1955; Burnstock 1959*a*, 1959*b*; Bullock 1963; Yamamoto 1966; Iwai 1968*a*, 1968*b*; Kimura 1973; Anderson and Mitchum 1974; Kimura and Kudo 1975; Ezeasor 1978, 1981*a*, 1981*b*; Ezeasor and Stokoe 1980*a*, 1980*b*). Many of these deal specifically with trout.

As in most carnivorous fishes, the digestive tract (gut) of trout is a relatively short, simple tube. The short esophagus joins the J-shaped stomach posteriorly. The longer anterior arm of the stomach is the cardiac portion and the shorter, posterior portion is the pyloric portion. Weinreb and Bilstad (1955) referred to the mid-area of the stomach, where the curvature occurs, as the transitional region. Immediately posterior to the stomach, and at the anterior end of the intestine, is a cluster of fingerlike diverticula, the pyloric caeca. The intestine forms a short bend at its anterior end, then continues as a straight tube to the vent or anus (Diagram 2).

The intestine of the trout is divided into two portions, often called the anterior and the posterior halves. Because of the significant differences between these halves in morphology, histology, and physiology, it seems desirable to use distinctive names for each part. Both Burnstock (1959*a*) and Bullock (1963) termed the more slender anterior half the intestine, and the enlarged posterior portion the rectum. There is also some justification for naming these two portions the small intestine (anterior) and the large intestine (posterior). However, we follow Weinreb and Bilstad (1955) in calling the anterior portion the ascending intestine and the posterior portion the descending intestine.

Oral Cavity

Teeth and taste buds are found primarily in the oral (buccal) cavity and the epidermal area of the pharynx (Plates 9 and 10). Although most fish do not have salivary glands (Anderson and Mitchum 1974), certain mucus secreting cells can be seen histologically. They often appear as vacuolated cells throughout the digestive tract, skin, and epidermis of the gills. In the "typical" teleost, the exposed surfaces of the teeth are covered with a highly mineralized substance known as enameloid (Poole 1967; Shellis and Miles 1974). This material differs microscopically from the enamel of higher vertebrates in that the enameloid is penetrated by fibers and cell processes from the dentine. In fishes the dentine is not as clearly differentiated from the enameloid as it is from the enamel in higher vertebrates. Shellis and Miles (1974) used the stainability of enameloid matrix with hematoxylin as an indicator of the onset of mineralization. The cells at the "base" of the tooth, where it contacts the dental papilla, are known as odontoblasts. These cells and those of the inner dental epithelium contribute protein to the enameloid matrix before mineralization begins.

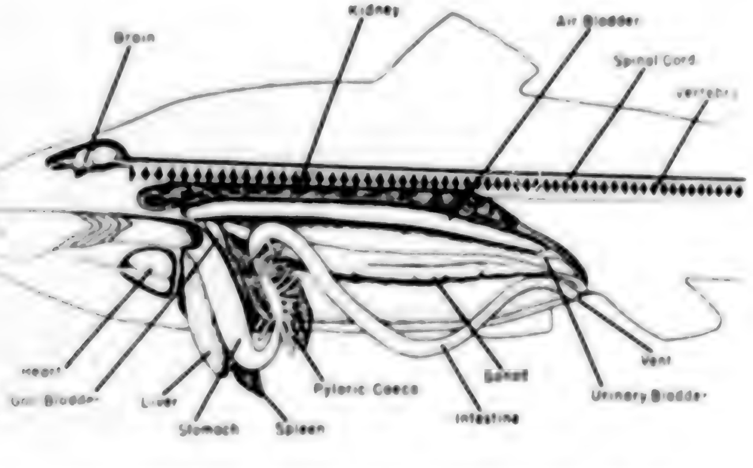


Diagram 2. Internal organs of a rainbow trout. (Adapted from Wales 1957)

BEST AVAILABLE COPY

Esophagus

The esophagus of rainbow trout consists of the four layers usually found in the alimentary tract of higher vertebrates: mucosa, submucosa, muscularis, and serosa (Weinreb and Bilstad 1955; Plate 11). The mucosal surface is undulated by large folds. These individual folds additionally contain many secondary folds (Plate 11, Fig. 3). Two glandular tissues occur in the mucosa: esophageal and serous cardiac. The mucus-secreting esophageal glands are anterior to the pneumatic duct and the serous glands are posterior to the duct and are "continuous with the similar glands of the cardiac stomach" (Weinreb and Bilstad 1955). Some investigators have reported the absence of submucosa, muscularis mucosa, stratum compactum, or stratum granulosum in the esophagus of brown trout, *Salmo trutta* (Burnstock 1959*a*) and rainbow trout (Anderson and Mitchum 1974). We found that, although these features may be lacking in young trout 3–4 months old (Plate 11), some elements of most of these areas are present in older fish, particularly in the distal or posterior end of the esophagus. The submucosa appears as a layer of loose connective tissue interspersed with fibroblasts. In the two-layered muscularis, the outer muscularis longitudinalis is not as prominent as the thick inner muscularis circularis. The serosa is usually thin and composed of methothelial cells and loose connective tissue. Intercellular mucous cells and wandering lymphocytes (Plate 15, Fig. 4) occur in the surface epithelium throughout the intestine.

Stomach

The stomach may be divided into three regions: cardiac (anterior), transitional (mid), and pyloric (posterior). All four layers (mucosa, submucosa, muscular coat, and serosa) are found in the stomach. The mucosa of the cardiac region (Plate 12) comprises the surface epithelium, the serous cardiac glands, lamina propria, stratum granulosum, stratum compactum, and muscularis mucosa. The cardiac glands form gastric pits that frequently extend into one-third of the mucosa (Anderson and Mitchum 1974; Plate 12, Fig. 1). These gland cells are serous and are very similar to the chief cells of other animals (Weinreb and Bilstad 1955). In young fish the stratum granulosum, with its granular cells (Plate 12, Figs. 2 and 3), is generally both external (stratum granulosum externum) and internal (stratum granulosum internum) to the collagenous stratum compactum (Kimura and Kudo 1975; Ezeasor and Stokoe 1980*b*). In older fish these cells are dispersed among the much diffused stratum compactum (Anderson and Mitchum 1974). As mentioned previously, this variability apparently is a function of age. The staining characteristics of granular cells also seem to vary with the species of fish and techniques used (Weinreb and Bilstad 1955). In trout fixed in Bouin-Hollande fluid, these cells are characteristically eosinophilic when stained with Masson's trichrome (Plates 14 and 17). Although the function of these cells is still not clear, Ezeasor and Stokoe (1980*b*) suggested that they are associated in some way with the body defense mechanism. This is an interesting observation, since the granular cells are extensively involved in infectious hematopoietic necrosis, a viral disease of trout and salmon. Histopathological changes in the cells are considered pathognomonic in juvenile fish affected with the disease (Yasutake 1975, 1979).

The muscularis mucosa is a thin layer of smooth muscle fibers. The submucosa adjacent to it is also thin, consisting mostly of loose connective tissue with some muscle fibers and blood vessels. The pyloric region of the stomach is basically similar to the cardiac stomach, except that it lacks the cardiac glands (Plate 13). Pyloric glands may or may not be seen in routine histological sections.

Intestine

Unlike the wall of the stomach, the wall of the intestine does not include a submucosa or muscularis mucosa. However, the stratum compactum and stratum granulosum are prominent in the mucosa (Plates 16 and 17). The muscularis and serosa of the ascending and descending intestine are similar, although the muscularis is a little thinner in the latter section. Both the circularis and longtitudinalis muscles are much thinner than those in the stomach or the esophagus. The goblet cells are much less apparent in the descending region.

Pyloric Caeca

Since, embryologically, the pyloric caeca are only extensions of the ascending intestine, the walls of the diverticula are histologically similar to those of the intestine; however, the caecal wall is generally narrower than the wall of the intestine (Plate 15).

Rectum

The outstanding feature of the rectum is the presence of the annulospiral septa extending into the lumen (Burnstock 1959*a*). In young fish, 3–4 months old, the spiraling of these septa is less pronounced (Plate 18, Fig. 1).

Liver

Grossly, the liver in trout is not generally arranged in distinct lobes, as it is in mammals. It is usually close to the transverse septum which separates the peritoneal cavity from the pericardial cavity (Plate 19, Fig. 1) and is on the left side in the abdominal cavity. The tissue morphology is highly complicated (Diagram 3). All vertebrate livers are constructed on one basic plan. The branching tunneled

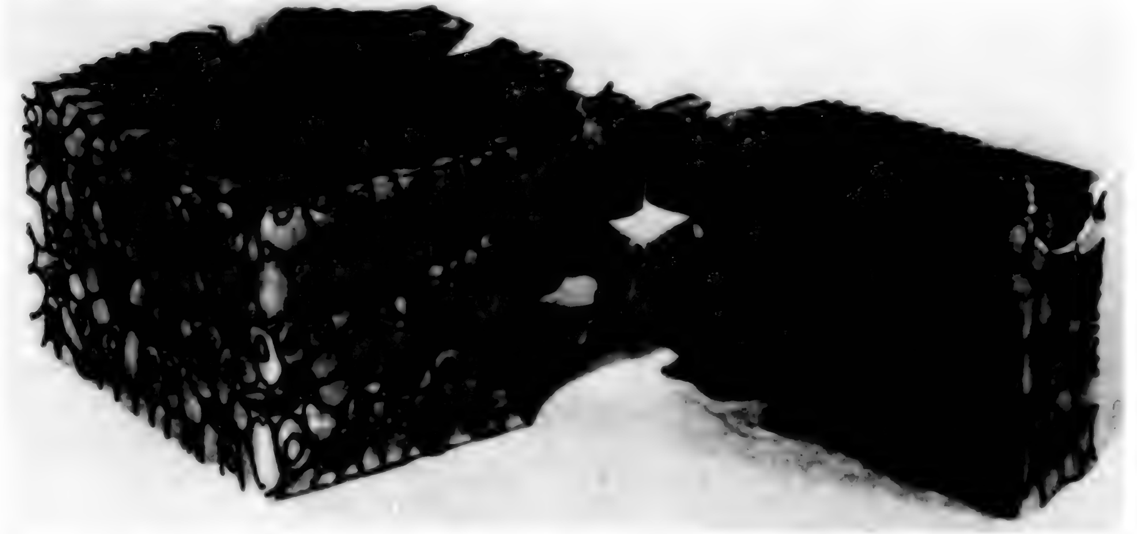


Diagram 3. Wax-plate reconstruction of normal liver from trout, showing typical arrangement of cell plates, two cells thick. Although true hepatic cords are not obvious, neither are they rare, on careful microscopic examination. (Courtesy of Dr. R. C. Simon)

maze of sinusoids is suspended in an intricate network of connecting cells. The cellular wall in fish, unlike the cellular walls in mammalian hepatic tissue, is usually two cells thick, as it is in most lower vertebrates (Elias and Bengelsdorf 1952; Elias 1955).

Histologically, the lobules are not as well defined as they are in livers of higher vertebrates. Their outlines are diffuse, but they are readily identified (Simon et al. 1967) by the central veins (Plate 19, Fig. 1) and hepatic triads (Plate 19, Fig. 5).

The liver is supplied with venous blood by the hepatic portal system, coming from the alimentary tract, and arterial blood from the hepatic artery. After passing through the myriad of veins and venules, the blood flows between the double-celled laminae or cords (Plate 19, Figs. 3 and 5), back into the venules and branches of the hepatic veins, and thence to the heart. In trout fingerlings, the blood vessels in the liver are thin-walled; even the wall of the hepatic artery is not much thicker than the corresponding vein returning blood to the heart. However, differences between the two systems soon develop and the collagen-filled strands of connective tissue thicken, so that in liver sections of yearling trout the differences between the arteries and veins are readily apparent. The endothelial cell nuclei project into the lumen of the arterioles in a unique and characteristic manner (Plate 19, Fig. 1). The connective tissue supporting and reinforcing the arterial walls extends out from the vessels and lines the wall of the liver cords. In sections stained with a tri-chrome technique, these green collagenous "membranes" can be seen between the sinusoids and the parenchymal cells of the liver cords. The hepatic parenchymal cells, which compose most of the liver volume, are relatively small and stain deeply. These cells are highly variable polygons that may be greatly distended by glycogen deposits or be free of stored foods. Wide variation in the content of these cells is normal, and dissimilarity in liver sections from any group of fish is the rule rather than the exception.

Biliary Tissue

Partly hidden beneath the liver is the gall bladder, connected to the liver by the afferent bile duct and to the pyloric end of the stomach by the efferent bile duct. The ducts of the biliary system are easily distinguished from blood vessels by the linings of cuboidal or columnar epithelial cells and by the lack of blood cells within their lumen (Plate 20).

Pancreas

Pancreatic tissue in trout, as in many other teleosts, is diffused throughout the adipose tissue that surrounds the pyloric caeca (Plates 21 and 22). The major portion of this tissue is composed of basophilic cells, which are arranged in spherical clusters and morphologically resemble the typical vertebrate pancreatic acinar cells (Anderson and Mitchum 1974). These triangular acinar cells have basally located, well-defined nuclei and nucleoli and apical cytoplasm with many eosinophilic zymogen granules (Plate 22c). Digestive enzymes secreted from these cells are carried into the ascending intestine through a series of ducts;

therefore it is designated the exocrine tissue, as opposed to the ductless endocrine tissue. The digestive enzymes are responsible for the breakdown of proteins, fats, and carbohydrates (Harder 1975).

The endocrine tissue of the pancreas occurs in microscopic clusters of glandular cells referred to as islets of Langerhans or Brockmann bodies. The shape, size, and number of these bodies in the pancreas are highly variable. In salmonids they are scattered throughout the pancreas, whereas in some fishes, like the channel catfish (*Ictalurus punctatus*) there are aggregations of cells known as "principal islets." The microscopic structure of the trout islet appears as a compact aggregation of glandular cells, each with a large, distinct nucleus. Actually the islets are composed of cords of cells interspersed with blood sinuses. All vertebrate islets, except those in the cyclostomes, are generally recognized as having three functionally independent cell types: glucagon producing A-cells; insulin producing B-cells; and islet hormone producing D-cells (Epple 1969, 1973). The X-cell, a fourth islet hormone producing cell, is also believed to occur in many species of fish (Brinn 1973; Epple and Lewis 1973).

Insulin from teleosts differs in its amino acid sequence from mammalian insulin; however, the consensus is that teleost insulin is necessary for maintenance of the blood sugar level. Removal of the islet tissue, where this is feasible, leads to hyperglycemia, glucosuria, and an increase in liver lipid. In the trout the extremely small size of the islets and their wide distribution makes surgical removal impossible. Other approaches, such as alloxan injection, have led to equivocal results. Administration of exogenous insulin has a hyperglycemic effect. Usually the glycogen content of the liver and muscle is increased.

Despite the considerable work that has been done with insulin in fish, its physiological role is not yet fully understood.

Swim Bladder (Gas Bladder)

It may seem out of place to include the swim bladder, also known as gas or air bladder, among the component structures of the alimentary tract; however, this bladder is actually a part of the esophagus. A pouch that develops from the dorsal surface of the esophagus is open during the late embryonic and early post-embryonic periods, and air can be gulped from the surface by the young fish and forced into the bladder to provide buoyancy. This opening is soon closed by the sphincter muscle at its juncture with the esophagus. Weinreb and Bilstad (1955) noted that "The swim bladder consists of three coats: the mucosa, muscular coat, and outer fibrous coat" (Plate 23). These coats become greatly distended when the bladder is filled with air. Food of very young trout occasionally enters the swim bladder; it is not digested there, and may serve as a medium for bacterial or fungal infection (Ross et al. 1975). Swim bladders of some teleosts have a rete mirabile, a gas secretory complex composed of closely associated arterial and venous capillaries (Jasinski and Kilarski 1971; Grizzle and Rogers 1976). This tissue is also associated with the choroid coat of the eye (Lagler et al. 1977).

References

Al-Hussaini, A. H. 1945. The anatomy and histology of the alimentary tract of *Scarus sordidus*. Bull. Inst. Egypte 27: 349–377.

Al-Hussaini, A. H. 1946. The anatomy and histology of the alimentary tract of the bottomfeeder, *Mulloides auriflamma* (Forsk.). J. Morphol. 78: 121–158.

Al-Hussaini, A. H. 1949*a*. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits. Part I. Anatomy and histology. Q. J. Microsc. Sci. 90: 109–140.

Al-Hussaini, A. H. 1949*b*. On the functional morphology of the alimentary tract of some fish in relation to differences in their feeding habits. Part II. Cytology and physiology. Q. J. Microsc. Sci. 90: 323–354.

Anderson, B. G., and D. L. Mitchum. 1974. Atlas of trout histology. Wyo. Game Fish Dep., Bull. 13. 110 pp.

Barbetta, F. 1962. Mucosal cells and mucoids in the gastric epithelium of fishes. Ann. Histochem. 1: 25–31.

Baumgarten, H. G. 1965. On the muscles and nerves in the intestinal wall of tenches. Z. Zellforsch. Mikrosk. Anat. 68: 116–137.

Bell, G. R., and J. E. Bateman. 1960. Some radiographic observations on the gastrointestinal and urinary systems of anesthetized Pacific salmon *Oncorhynchus*. Can. J. Zool. 38: 199–202.

Bellisio, N. B. 1965. Anatomia e histologia del tracto digestivo de algunos pimelodidos argentinos. An. Segund. Congr. Lat.-Am. Zool. 2: 107–123.

Bergeron, T., and B. Woodward. 1982. The development of the stratum granulosum of the small intestine of the rainbow trout (*Salmo gairdneri*). Can. J. Zool. 60: 1513–1515.

Bergot, P., A. Solari, and P. Luquet. 1975. A comparison of absorptive surfaces of pyloric caeca and intestine in the rainbow trout (*Salmo gairdneri*, Richardson). Ann. Hydrobiol. 6: 27–43.

Berlin, J. D., and J. M. Dean. 1967. Temperature-induced alterations in hepatocyte structure of rainbow trout *Salmo gairdneri*. J. Exp. Zool. 164: 117–132.

Berry, P. Y., and M. P. Low. 1970. Comparative studies on some aspects of the morphology and histology of *Ctenopharyngodon idellus*, *Aristichthys nobilis*, and their hybrid (Cyprinidae). Copeia 1970: 708–726.

Bishop, C., and P. H. Odense. 1966. Morphology of the digestive tract of the cod, *Gadus morhua*. J. Fish. Res. Board Can. 23: 1607–1615.

Blake, I. H. 1930. Studies on the comparative histology of the digestive tube of certain teleost fishes. I. A predaceous fish, the sea bass *Centropristes striatus*. J. Morphol. 50: 39–70.

Blake, I. H. 1936. Studies on the comparative histology of the digestive tube of certain teleost fishes. III. A bottom-feeding fish, the sea robin (*Prionotus carolinus*). J. Morphol. 60: 77–102.

Boldyreff, E. B. 1935. A microscopic study of the pancreas in fishes; especially those of the orders Haplomi and Cyprinodontes. Copeia 1935: 23–34.

Bolton, L. L. 1933. Basophil (mast) cells in the alimentary canal of salmonid fishes. J. Morphol. 54: 549–560.

Boquist, L., and G. Patent. 1971. The pancreatic islets of the teleost *Scorpaena scropha*. An ultrastructural study with particular regard to fibrillar granules. Z. Zellforsch. Mikrosk. Anat. 115: 416–425.

Brinn, J. E., Jr. 1973. The pancreatic islets of bony fishes. Am. Zool. 13: 653–665.

Brooks, R. E. 1970. Ultrastructure of the physostomatous swimbladder of rainbow trout *Salmo gairdneri*. Z. Zellforsch. Mikrosk. Anat. 106: 473–483.

Bucke, D. 1971. The anatomy and histology of the alimentary tract of the carnivorous fish, the pike *Esox lucius* L. J. Fish Biol. 3: 421–431.

Bulger, R. E. 1963. Fine structure of the rectal (salt-secreting) gland of the spiny dogfish, *Squalus acanthias*. Anat. Rec. 147: 95–127.

Bullock, W. L. 1963. Intestinal histology of some salmonid fishes with particular reference to the histopathology of acanthocephalan infections. J. Morphol. 112: 23–44.

Bullock, W. L. 1967. The intestinal histology of the mosquitofish, *Gambusia affinis* (Baird and Girard). Acta Zool. (Stockh.) 48: 1–17.

Burnstock, G. 1959*a*. The morphology of the gut of the brown trout, *Salmo trutta*. Q. J. Microsc. Sci. 100: 183–198.

Burnstock, G. 1959*b*. The innervation of the gut of the brown trout, *Salmo trutta*. Q. J. Microsc. Sci. 100: 199–220.

Byczkowska-Smyk, W. 1965. The structure of cells in the liver of the pondloach (*Misgurnus fossilis*). Acta Biol. Cracov. Ser. Zool. 8: 41–54.

Byczkowska-Smyk, W. 1968. Observations of the ultrastructure of the hepatic cells of the burbot *Lota lota*. Zool. Poln. 18: 287–298.

Chaicharn, A., and W. L. Bullock. 1967. The histopathology of acanthocephalan infections in suckers with observations on the intestinal histology of two species of catostomid fishes. Acta Zool. (Stockh.) 48: 19–42.

Chapman, G. B. 1981. Ultrastructure of the liver of the fingerling rainbow trout *Salmo gairdneri* Richardson. J. Fish Biol. 18: 553–567.

Ch[illegible]drey, H. S., and O. P. Khandelwal. 1961. The anatomy and histology of the alimentary tract of *Oreinus plagiostomus* (Keckel). Annot. Zool. Jpn. 32: 139–152.

Cheng, L. T. 1931. A preliminary note on the epithelium and its adjacent structures of the fishes' stomach in spring and winter. Contrib. Biol. Lab. Sci. Soc. China 7: 305–313.

Chester Jones, I., D. K. O. Chan, I. W. Henderson, and J. N. Ball. 1969. The adrenocortical steroids, adrenocorticotropin and the corpuscles of Stannius. Pages 321–376 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

Ciullo, R. H. 1975. Intestinal histology of *Fundulus heteroclitus* with observations on the effects of starvation. Pages 733–767 *in* W. E. Ribelin and G. Migaki, eds. The pathology of fishes. University of Wisconsin Press, Madison.

Clarke, A. J., and D. M. Witcomb. 1980. A study of the histology and morphology of the digestive tract of the common eel (*Anguilla anguilla*). J. Fish Biol. 16: 159–170.

Copeland, D. E. 1969. Fine structural study of gas secretion in the physoclistous swim bladder of *Fundulus heteroclitus* and *Gadus callarias* and in the euphysoclistous swim bladder of *Opsanus tau*. Z. Zellforsch. Mikrosk. Anat. 93: 30[illegible]–331.

Curry, E. 1939. The histology of the digestive tube of the carp *Cyprinus carpio communis*. J. Morphol. 65: 53–78.

Dawes, B. 1929. The histology of the alimentary tract of the plaice *Pleuronectes platessa*. Q. J. Microsc. Sci. 73: 243–274.

de Oliveira e Silva, S. L. 1966. Histologic aspects of the digestive tract (stomach, intestine) of *Plecostomus* sp. (Pisces Actinopterygii, Loricariidae). Atlas Soc. Biol., Rio de J. 9: 63–68.

Elias, H. 1955. Origin and early development of the liver in various vertebrates. Acta Hepato-splenol. (Stuttg.) 3: 1–56.

Elias, H., and H. Bengelsdorf. 1952. The structure of the liver of vertebrates. Acta Anat. 14: 297–337.

Epple, A. 1968. Comparative studies on the pancreatic islets. Endocrinol. Jpn. 15: 107–122.

Epple, A. 1969. The endocrine pancreas. Pages 275–319 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

Epple, A., and T. L. Lewis. 1973. Comparative histophysiology of the pancreatic islets. Am. Zool. 13: 567–590.

Ezeasor, D. N. 1978. The gut of the rainbow trout (*Salmo gairdneri*): a gross, histological, and ultrastructural study with some aspects of functional significance. Ph.D. Thesis. University of Edinburgh, Scotland.

Ezeasor, D. N. 1981*a*. The fine structure of the gastric epithelium of the rainbow trout, *Salmo gairdneri*, Richardson. J. Fish Biol. 19: 611–627.

Ezeasor, D. N. 1981*b*. Micromorphological observations on the nervous elements in the rectal mucosal folds of the rainbow trout (*Salmo gairdneri*, Rich.). Z. Mikrosk. Anat. Forsch. 95: 692–700.

Ezeasor, D. N., and W. M. Stokoe. 1980*a*. Scanning electron microscopic study of the gut mucosa of the rainbow trout *Salmo gairdneri* Richardson. J. Fish Biol. 17: 529–539.

Ezeasor, D. N., and W. M. Stokoe. 1980*b*. A cytochemical, light and electron microscopic study of the eosinophilic granule cells in the gut of the rainbow trout, *Salmo gairdneri* Richardson. J. Fish Biol. 17: 619–634.

Ezeasor, D. N., and W. M. Stokoe. 1981. Light and electron microscopic studies on the absorptive cells of the intestine, caeca, and rectum of the adult rainbow trout, *Salmo gairdneri*, Rich. J. Fish Biol. 18: 527–544.

Fahlen, G. 1965. Histology of the posterior chamber of the fish swimbladder of *Argentina*. Nature (Lond.) 207 (4992): 94–95.

Fahlen, G. 1967*a*. Morphological aspects of the hydrostatic function of the gas bladder of *Clupea harengus* L. Acta Univ. Lund., Sect. II 1: 1–37.

Fahlen, G. 1967*b*. Morphology of the gas bladder of *Coregonus lavaretus* L. Acta Univ. Lund., Sect. II 28: 1–37.

Fahlen, G. 1971. The functional morphology of the gas bladder of the genus *Salmo*. Acta Anatom. 78: 161–184.

Faller, A., and R. Lange. 1969. Kombinierte licht- und elektronenmikroskopische Analyse des Zellbildes in den Langerhansschen Inseln des Karpfens. Arch. Histol. Jpn. 31: 73–80.

Fange, R. 1953. The mechanisms of gas transport in the euphysoclist swimbladder. Acta Physiol. Scand., vol. 30. Suppl. 110. 133 pp.

Fawcett, D., and J. Wittenberg. 1959. The fine structure of capillaries in the rete mirabile of the swim bladder of *Opsanus tau*. Anat. Rec. 133: 274.

Ferri, S. 1981. Ultrastructural identification of smooth muscle cells in the perisinusoidal space of a freshwater teleost liver. Arch. Anat. Microsc. Morph. Exp. 70: 245–250.

Ferri, S., and A. Sesso. 1981*a*. Ultrastructural study of Kupffer cells in teleost liver under normal and experimental conditions. Cell Tissue Res. 220: 387–392.

Ferri, S., and A. Sesso. 1981*b*. Ultrastructural study of the endothelial cells in teleost liver sinusoids under normal and experimental conditions. Cell Tissue Res. 219: 649–657.

Gammon, R. L. 1970. The gross and microanatomy of the digestive tract and the pancreas of the channel catfish, *Ictalurus punctatus*. M. S. Thesis. Kansas State University, Manhattan. 52 pp.

Garant, P. R. 1970. An electron microscopic study of the crystal-matrix relationship in the teeth of the dogfish *Squalus acanthias* L. J. Ultrastruct. Res. 30: 441–449.

Garant, P. R. 1971. Cytodifferentiation of the ectodermal component of developing teeth in the pickerel, *Esox lucius*. Int. Assoc. Dent. Res. Preprinted abstracts. 49th General Meeting. (Abstr. 121)

Gauthier, G. F., and S. C. Landis. 1972. The relationship of ultrastructural and cytochemical features to absorptive activity in the goldfish intestine. Anat. Rec. 172: 675–701.

Gawrilenko, A. 1910. Die Entwickelung des Geruchsorgans bei *Salmo salar*. Anat. Anz. 36: 411–427.

Gohar, H. A. F., and A. F. A. Latif. 1961. The histology of the alimentary tract in representative scarid and labrid fishes (from the Red Sea). Publ. Mar. Biol. Stn. Al Ghardaqa 11: 95–106.

Greene, C. W. 1912*a*. The absorption of fats by the alimentary tract, with special reference to the function of the pyloric caeca in the king salmon, *Oncorhynchus tschawytscha*. Trans. Am. Fish. Soc. 4: 261–270.

Greene, C. W. 1912*b*. Anatomy and histology of the alimentary tract of the king salmon. Bull. U.S. Bur. Fish. 32: 75–101.

Greene, C. W. 1913. The fat absorping function of the alimentary tract of the king salmon. Bull. U.S. Bur. Fish. 33: 149–176.

Grizzle, J. M., and W. A. Rogers. 1976. Anatomy and histology of the channel catfish. Auburn University Agricultural Experiment Station, Auburn, Alabama. 94 pp.

Gupta, O. P. 1971. Studies on the morphology, histology, and the swallowing mechanism of the digestive tract of a carnivorous fish, *Xenentodon cancila* (Han.). Okajima, Folia Anat. Jpn. 48: 29–51.

Hale, P. A. 1965. The morphology and histology of the digestive systems freshwater teleosts, *Peocilia reticulata* and *Gasterosteus aculeatus*. J. Zool. Proc. Zool. Soc. Lond. 146: 132–149.

Harder, W. 1975. Anatomy of fishes. E. Schweizerbart'sche Verlagsbuchhandlung (Nagele u. Obermiller) Stuttgart. Part I: Text 612 pp. (Transl. from German)

Henderson, V. 1975. Scanning electron microscopy of the air bladder in the spotted gar, *Lepisosteus occulatus*. J. Morphol. 147: 293–298.

Hendricks, J. D., L. J. Hunter, and J. H. Wales. 1976. Postmortem bile damage to rainbow trout (*Salmo gairdneri*) livers. J. Fish. Res. Board Can. 33: 2813–2816.

Herold, R. C. B. 1970. The fine structure of vasodentine in the teeth of the white hake, *Urophycis tenuis* (Pisces, Gadidae). Arch. Oral Biol. 15: 311–322.

Herold, R. C. B. 1974. Ultrastructure of odontogenesis in the pike *Esox lucius*. Role of dental epithelium and formation of enameloid layer. J. Ultrastruct. Res. 48: 435–454.

Hinton, D. E., M. W. Kendall, and B. B. Silver. 1973. Use of histologic and histochemical assessments in the prognosis of the effects of aquatic pollutants. Pages 194–208 *in* Biological methods for the assessment of water quality. American Society for Testing and Materials, Philadelphia, ASTM STP 528.

Hinton, D. E., and C. R. Pool. 1976. Ultrastructure of the liver in channel catfish *Ictalurus punctatus* (Rafinesque). J. Fish Biol. 8: 209–220.

Hinton, D. E., R. L. Snipes, and M. W. Kendall. 1972. Morphology and enzyme histochemistry in the liver of largemouth bass (*Micropterus salmoides*). J. Fish. Res. Board Can. 29: 531–534.

Hirano, S., and Y. Honma. 1972. Cytology of the endocrine pancreas of the bluefin tuna *Thunnus thynnus* caught in the Japan Sea. Annu. Rep. Sado Mar. Biol. Stn., Niigata Univ. 2: 1–8.

Honma, Y., and E. Tamura. 1968. Studies on Japanese chars of the genus *Salvelinus*. V. Cytology of the pancreatic islets in the Nikko-iwana, *Salvelinus leucomaenis pluvius* (Hilgendorf). Bull. Jpn. Soc. Sci. Fish. 34: 555–561.

Inui, Y., and S. Egusa. 1967. Histological changes observed in glass eel liver during starvation. Bull. Jpn. Soc. Sci. Fish. 33: 181–189.

Ishida, J. 1935–36. Ciliated intestinal epithelium in teleosts. Annot. Zool. Jpn. 15: 158–160.

Ishida, J., and M. Sato. 1960. The anatomical and histological observation of the alimentary tract of a catfish, *Parasilurus asotus* L. Sci. Rep. Hirosaki Univ. 7: 57–63.

Ishii, K., and K. Yamamoto. 1970. Sexual differences of the liver cells in the goldfish *Carassius auratus* L. Bull. Fac. Fish. Hokkaido Univ. 21: 161–167.

Isokawa, S., G. Van Huysen, and T. Kosakai. 1965. Telemicroscopy of fish tooth tubular enamel. J. Dent. Res. 44: 449.

Iwai, T. 1967*a*. The comparative study of the digestive tracts of teleost larvae. I. Fine structure of the gut epithelium in larvae of ayu. Bull. Jpn. Soc. Sci. Fish. 33: 489–496.

Iwai, T. 1967*b*. The comparative study of the digestive tracts of teleost larvae. II. Ciliated cells of the gut epithelium in pond smelt larvae. Bull. Jpn. Soc. Sci. Fish. 33: 116–119.

Iwai, T. 1968*a*. Fine structure and absorption pattern of intestinal epithelial cells in rainbow trout alevins. Z. Zellforsch. Mikrosk. Anat. 91: 366–379.

Iwai, T. 1968*b*. Notes on the pear-shaped cell (rodlet cell) in the epithelium of the digestive tract of fishes. Bull. Jpn. Soc. Sci. Fish. 34: 133–137.

Iwai, T. 1968*c*. The comparative study of the digestive tract of teleost larvae. IV. Absorption of fat by the gut of halfbeak larvae. Bull. Jpn. Soc. Sci. Fish. 34: 871.

Iwai, T. 1968*d*. The comparative study of the digestive tract of teleost larvae. V. Fat absorption in the gut epithelium of goldfish larvae. Bull. Jpn. Soc. Sci. Fish. 34: 973.

Iwai, T., and M. Tanaka. 1968. The comparative study of the digestive tract of teleost larvae. III. Epithelial cells in the posterior gut of halfbeak larvae. Bull. Jpn. Soc. Sci. Fish. 34: 44–48.

Janssen, B. O., and R. Olsen. 1960. The cytology of the caecal epithelial cells of *Perca*. Acta Zool. (Stockh.) 41: 267–276.

Jasinski, A., and W. Kilarski. 1969. On the fine structure of the gas gland in some fishes. Z. Zellforsch. Mikrosk. Anat. 102: 333–356.

Jasinski, A., and W. Kilarski. 1971. Capillaries in the rete mirabile and in the gas gland of the swim bladder in fishes, *Perca fluviatilis* L. and *Misgurnus fossilis* L. Acta Anat. 78: 210–223.

Jilek, R. 1979. Intestinal histology of *Dorosoma cepedianum*. J. Fish Biol. 14: 125–128.

Johansson, N. 1965. Histological studies of the livers from 1½ year old salmon *Salmo salar* L. raised on different diets. Swedish Salmon Res. Inst. Rep. No. 9. Alvkarleo, Sweden, University of Gothenburg. 9 pp.

Jones, F. R., and N. B. Marshall. 1953. The structure and function of the teleostean swimbladder. Biol. Rev. Cambridge Physiol. Soc. 28: 16–83.

Jordan, H. E., and C. C. Speidel. 1923–25. Studies on lymphocytes. II. The origin, function and fate of lymphocytes in fishes. J. Morphol. 38: 529–549.

Kapoor, B. G. 1954. The anatomy and histology of the pharyngeal organ in *Hilsa ilisha* (Ham.). J. Zool. Soc. India 6: 167–176.

Kapoor, B. G., H. Smit, and I. A. Verighina. 1975. The alimentary canal and digestion in teleosts. Pages 109–239 *in* F. S. Russell and M. Yonge, eds. Advances in marine biology, vol. 13. Academic Press, New York.

Khalilov, F. K. 1968. Some material on the histology and histochemistry of the pancreas and liver of teleost fishes. Vopr. Ikhtiol. 8: 312–317.

Khanna, S. S. 1963. Histology and cytology of the pancreas of some freshwater fishes. Indian Zool. Mem. 7: 1–19.

Khanna, S. S., and B. K. Mehratra. 1969. Histology of the islets of Langerhans in normal and alloxan-treated fresh water catfish, *Clarias batrachus* (L.). Zool. Beitr. 14: 489–497.

Kitamikado, M., and S. Tachino. 1961. Digestive enzymes of rainbow trout. III. Esterases. Chem. Abstr. 55: 5789e.

Kimura, N. 1973. Fine structure of the epithelial cells in the pyloric caecum of the rainbow trout, *Salmo gairdneri*. Jpn. J. Ichthyol. 20: 13–24.

Kimura, N., and S. Kudo. 1975. Fine structure of the stratum granulosum of the pyloric caeca of the rainbow trout. Jpn. J. Ichthyol. 22: 16–22.

Klein, C., and R. H. Lange. 1977. Principal cell types in the pancreatic islet of a teleost fish, *Xiphophorus helleri* H. Cell Tissue Res. 176: 529–551.

Kobayashi, K., and Y. Takahashi. 1970. Light and electron microscope observations on the islets of Langerhans in *Carassius carassius longsdorfii*. Arch. Histol. Jpn. 31: 433–454.

Kobayashi, K., and Y. Takahashi. 1974. Fine structure of Langerhans islet cells in a marine teleost *Conger japonicus*, Bleeker. Gen. Comp. Endocrinol. 23: 1–18.

Korovina, V. M., and N. E. Vasil'eva. 1971. Comparative histologic studies on the mid-intestine of certain members of the salmon family (Salmonidae). Vopr. Ikhtiol. 11: 502–508.

Krementz, A. B., and C. B. Chapman. 1975. Ultrastructure of the posterior half of the intestine of the channel catfish, *Ictalurus punctatus*. J. Morphol. 145: 441–482.

Kudinskii, O. Yu. 1968. Microscopic anatomy of the digestive tract of Atlantic salmon (*Salmo salar*) fingerlings. Tr. Murm. Morsk. Biol. Inst. 12: 112–119.

Kudo, S., and Y. Takahashi. 1973. New cell types of the pancreatic islets in the crucian carp, *Carassius carassius*. Z. Zellforsch. Mikrosk. Anat. 146: 425–438.

Kvam, T. 1950. The development of mesodermal enamel on piscine teeth. K. Nor. Vidensk. Selsk. Forh. 23: 7-115.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. R. M. Passino. 1977. Ichthyology, 2nd ed. John Wiley & Sons, Inc., New York. 545 pp.

Lawson, R., and B. F. G. Manly. 1973. Tooth growth and replacement in *Ctenolucius hujeta*, a neotropical characoid fish. J. Morphol. 141: 383–394.

Levi, G. 1940. Etudes sur le developpement des dents chez les Teleosteens. III. Developpement de dents de substitution de *Merluccius*, *Chrysophrys*, *Cepola*, *Lophius*. Arch. Anat. Microsc. (Paris) 35: 101-146.

Ling, E. A., and C. K. Tan. 1975. Fine structure of the gastric epithelium of the coral fish, *Chelmon rostratus*, Cuvier. Okajimas Folia Anat. Jpn. 51: 285–310.

Lovern, J. A. 1934. Fat metabolism in fishes. V. The fat of the salmon in its freshwater stages. Biochem. J. 28: 1961-1963.

Maksimovich, A. A., and G. K. Korotaev. 1969. Spawning-connected changes in the fine structure of the liver cells' nuclei and nucleoli in the Pacific salmon. Tsitologiya 11: 1393–1400.

Maksimovich, A. A., A. D. Barthova, V. V. Plyusnin, V. M. Bondareva, L. P. Plisetskaya, and E. M. Plisetskaya. 1978. Ultrastructure and function of pancreatic B-cells in the humpback salmon during spawning migration. Biol. Morya (Vladivost.) 6: 61–69. [In Russian with Russian and English summaries]

McVay, J. A., and H. W. Kaan. 1940. The digestive tract of *Carassius auratus*. Biol. Bull. (Woods Hole) 78: 53–67.

Mohd, M. S. 1962. Comparative morphology and histology of the alimentary canals in certain groups of Indian teleosts. Acta Zool. (Stockh.) 43: 79–133.

Morris, S. M., and J. T. Albrecht. 1979. Ultrastructure of the swim bladder of the goldfish, *Carassius auratus*. Cell Tissue Res. 198: 105–117.

Nakamura, M., and M. Yokote. 1971. Ultrastructural studies on the islets of Langerhans of the carp. Z. Anat. Entwicklungsgesch. 134: 61–72.

Nittinger, J. 1968. Histologische und histochemische Untersuchungen uber die Involution des Dottersacks bei *Lebistes reticulatus* (Peters) und *Salmo irideus* (Gibb). Zool. Jarb. Anat. 85: 245–325.

Noaillac-Depeyre, J., and N. Gas. 1978. Ultrastructural and cytochemical study of the gastric epithelium in a freshwater teleostean fish (*Perca fluviatilis*). Tissue & Cell 10: 23–37.

Nopanitya, W., J. Aghajanian, J. W. Grisham, and J. L. Carson. 1979. An ultrastructural study on a new type of hepatic perisinusoidal cell in fish. Cell Tissue Res. 198: 35–42.

Nopanitya, W., J. L. Carson, J. W. Grisham, and J. G. Aghajanian. 1979. New observations on the fine structure of the liver in goldfish (*Carassius auratus*). Cell Tissue Res. 196: 249–261.

Oguri, M. 1979. A histological study on the endocrine and exocrine glands of fish by Bowie's stain. Bull. Jpn. Soc. Sci. Fish. 45: 823–827.

Ostberg, Y., R. Fange, A. Mattisson, and N. W. Thomas. 1976. Light and electron microscopical characterizations of heterophilic granulocytes in the intestinal wall and islet parenchyma of the hagfish, *Myxine glutinosa* (Cyclostomata). Acta Zool. (Stockh.) 57: 89.

Ovalle, W. K., and S. L. Shinn. 1977. Surface morphology of taste buds in catfish barbels. Cell Tissue Res. 178: 375–384.

Pasha, K. 1964. The anatomy and histology of the alimentary canal of herbivorous fish *Tilapia mossambica* (Peters). Proc. Indian Acad. Sci. B54: 340–349.

Poole, D. F. G. 1967. Phylogeny of tooth tissues: enameloid and enamel in recent vertebrates, with a note on the history of cementum. Pages 111–149 *in* A. E. W. Miles, ed. Structural and chemical organization of teeth. Academic Press, New York.

Rahimullah (Quarishi), M. 1944. A comparative study of the morphology, histology and possible functions of the pyloric caeca in Indian fishes, together with a discussion on their homology. Ph.D. Thesis. University of Madras, India. 37 pp.

Rambout, J. H. W. M. 1977. Enteroendocrine cells in the digestive tract of *Barbus conchonius* (Teleostei, Cyprinidae). Cell Tissue Res. 185: 435–450.

Reifel, C. W., and A. A. Travill. 1977. Structure and carbohydrate histochemistry of the esophagus in ten teleostean species. J. Morphol. 152: 303–313.

Reifel, C. W., and A. A. Travill. 1978. Structure and carbohydrate histochemistry of the stomach in eight species of teleosts. J. Morphol. 158: 155–168.

Reutter, K., W. Breipohl, and G. J. Bijvank. 1974. Taste bud types in fishes. II. Scanning electron microscopical investigations on *Xiphophorus helleri* Heckel (Poeciliidae, Cyprinodontiformes, Teleostei). Cell Tissue Res. 153: 151-165.

Rogick, M. D. 1931. Studies on the comparative histology of the digestive tube of certain teleost fishes. II. A minnow *Campostoma anomalum*. J. Morphol. 52: 1–25.

Ross, A. J., W. T. Yasutake, and S. Leak. 1975. *Phoma herbarum*, a fungal plant saprophyte as a fish pathogen. J. Fish. Res. Board Can. 32: 1648–1652.

Saddler, J. B., and L. M. Ashley. 1960. Comparative histology of the pyloric caeca of certain teleost fish. Walla Walla Coll. Publ., Dep. Biol. Sci. Biol. Stn. 27: 1–23.

Sarbahi, D. S. 1951. Studies on the digestive tracts and the digestive enzymes of the goldfish, *Carassius auratus* (Linnaeus) and the largemouth black bass, *Micropterus salmoides* (Lacepede). Biol. Bull. (Woods Hole) 100: 244–257.

Sato, T., L. Herman, and P. J. Fitzgerald. 1966. The comparative ultrastructure of the pancreatic islets of Langerhans. Gen. Comp. Endocrinol. 7: 132–157.

Schliwa, M. 1975. Cytoarchitecture of surface layer cells of the teleost epidermis. J. Ultrastruct. Res. 52: 377–386.

Schmitz, E. H., and C. D. Baker. 1969. Digestive anatomy of the gizzard shad, *Dorosoma cepedianum* and the threadfin shad, *D. petenense*. Trans. Am. Microsc. Soc. 88: 525–546.

Shellis, R. P., and A. E. W. Miles. 1974. Autoradiographic study of the formation of enameloid and dentine matrices in teleost fishes using tritiated amino acids. Proc. R. Soc. Lond. B. Biol. Sci. 185: 51–72.

Simon, R. C., A. M. Dollar, and E. A. Smuckler. 1967. Descriptive classification on normal and altered histology of trout liver. Pages 18–28 *in* J. E. Halver and I. A. Mitchell, eds. Trout hepatoma research conference papers. U. S. Fish Wildl. Serv., Res. Rep. 70.

Singh, R. 1966. Morpho-histological studies of the alimentary canal *bagarius* (Ham.). Agra Univ. J. Res. 155: 69–81.

Sis, R. F., P. J. Ives, D. M. Jones, D. H. Lewis, and W. E. Haensly. 1979. The microanatomy of the oesophagus, stomach and intestine of the channel catfish, *Ictalurus punctatus*. J. Fish Biol. 14: 179–186.

Sivadas, P. 1964a. Absorption of fat in the alimentary canal of *Tilapia mossambica* (Peters) (Teleostei). J. Cell. Comp. Physiol. 65: 249–254.

Sivadas, P. 1964*b*. The occurrence of B-cells in the islets of Langerhans of *Tilapia mossambica* (Peters) (Teleostei). Gen. Comp. Endocrinol. 4: 295–298.

Smith, H. 1975. Eosinophilic granular cells of salmonids. M.S. Thesis. University of Stirling, Scotland.

Stolk, A. 1963. Pharyngeal glands in the mouthbreeding anabantid *Betta anabatoides* (Bleeker). Acta Morphol. Neerl. Scand. 5: 252–260.

Suyehiro, Y. 1942. A study on the digestive system and feeding habits of fish. Jpn. J. Zool. 10: 1–303.

Tamura, E., and Y. Honma. 1971. Histological changes in the organs and tissues of the gobiid fishes throughout the life-span: IV. Digestive organs of the ice-goby. Bull. Jpn. Soc. Sci. Fish. 37: 831–839.

Thomas, N. W. 1970. Morphology of endocrine cells in the islet tissue of the cod, *Gadus callarias*. Acta Endocrinol. 63: 671–695.

Twongo, T. K., and H. R. MacCrimmon. 1977. Histogenesis of the oropharyngeal and oesophageal mucosa as related to early feeding in rainbow trout, *Salmo gairdneri* Richardson. Can. J. Zool. 55: 116–128.

Vasil'eva, N. E., and V. M. Korvina. 1969. A comparative histological study of the mid-intestine in a number of Salmonidae. Vopr. Ikhtiol. 9: 191–196.

Verma, S. R., and M. P. Tyagi. 1974. A comparative histological study of the stomach of a few teleost fishes. Gegenbaurs Morphol. Jahrb. 120: 244–253.

Vickers, T. 1962. A study of the intestinal epithelium of the goldfish *Carassius auratus*: its normal structure, the dynamics of cell replacement, and the changes induced by salts of cobalt and manganese. Q. J. Microsc. Sci. 103: 93–110.

Wales, J. H. 1957. Trout of California. California Department of Fish and Game, Sacramento. 56 pp.

Wargo, A. A. 1978. Light and electron microscope studies of changes in gastric tissues of the channel catfish, *Ictalurus punctatus* (Rafinesque), as related to feeding times. Ph.D. Thesis. Georgetown University, Washington, D. C. 273 pp.

Watari, N., N. Tsukagoshi, and Y. Honma. 1970. The correlative light and electron microscopy of the islets of Langerhans in some lower vertebrates. Arch. Histol. Jpn. 31: 371–392.

Weinreb, E. L. 1959. Studies on the histology and histopathology of the rainbow trout, *Salmo gairdneri irideus*. II. Effects of induced inflammation and cortisone treatment on the digestive organs. Zoologica (N.Y.) 44: 45–52.

Weinreb, E. L., and N. M. Bilstad. 1955. Histology of the digestive tract and adjacent structures of the rainbow trout, *Salmo gairdneri irideus*. Copeia 1955: 194–204.

Weisel, G. F. 1962. Comparative study of the digestive tract of a sucker, *Catostomus catostomus*, and a predaceous minnow, *Ptychocheilus oregonense*. Am. Midl. Nat. 68: 334–346.

Weisel, G. F. 1973. Anatomy and histology of the digestive system of the paddlefish (*Polyodon spathula*). J. Morphol. 140: 243–255.

Yamamoto, T. 1966. An electron microscope study of the columnar epithelial cell in the intestine of freshwater teleosts: goldfish *Carassius auratus* and rainbow trout *Salmo irideus*. Z. Zellforsch. Mikrosk. Anat. 72: 66–87.

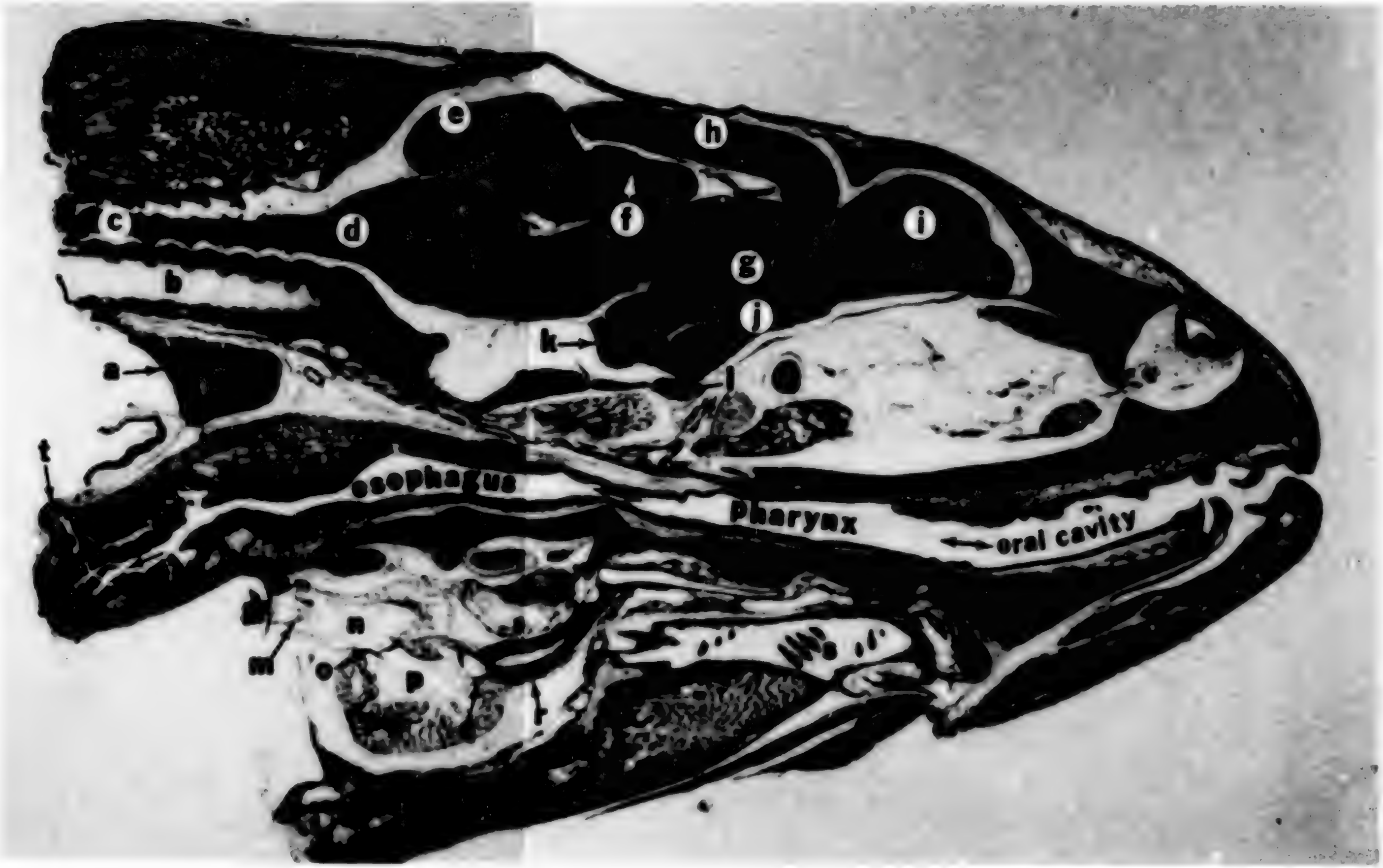
Yasutake, W. T. 1975. Fish virus diseases: Clinical, histopathological and comparative aspects. Pages 247–271 *in* A. E. Ribelin and G. Migaki, eds. The pathology of fishes. University of Wisconsin Press, Madison.

Yasutake, W. T. 1979. Histopathology of yearling sockeye salmon (*Oncorhynchus nerka*) infected with infectious hematopoietic necrosis (IHN). Fish Pathol. 14: 59–64.

Young, J. E., and W. Chavin. 1966. Histopathology of the islets of Langerhans, adrenals, liver and kidney of control and alloxan diabetic goldfish, *Carassius auratus* L. Am. Zool. 6: 562. (Abstr.)

Plate 9. Digestive Tract. Sagittal section through the head of a 3-month-old rainbow trout, showing the several regions of the gut between the mouth and the junction of the swim bladder. × 35.

a. Head kidney
b. Notochord
c. Spinal cord
d. Myelencephalon (medulla oblongata)
e. Metencephalon (cerebellum)
f. Cerebellar valvula
g. Diencephalon (between brain)
h. Mesencephalon (optic lobe)
i. Telencephalon (forebrain)
j. 3rd ventricle
k. Saccus vasculosus
l. Pituitary
m. Sino-atrial valve
n. Atrium
o. Atrio-ventricular valve
p. Ventricle
q. Ventriculo-bulbar valve
r. Bulbus arteriosus
s. Gills
t. Pneumatic duct



33

Plate 10. Teeth

Fig. 1. Sagittal section through the head of a 1-month-old rainbow trout. × 50.

- a. Emerging teeth of the vomer, dentary, and basihyal cartilages
- b. A portion of the optic nerve
- c. Oral cavity
- d. Oral valve

Fig. 2. Longitudinal section of a vomerine tooth of a 3-month-old rainbow trout. × 320.

- a. Dentine
- b. Enamel
- c. Pulp, composed of blood vessels, nerves, and connective tissue
- d. Oral epithelium

Fig. 3. Anterior maxillary tooth (not yet emerged from the dental cup) of a 3-month-old rainbow trout. × 320.

- a. Odontoblasts
- b. Dentine
- c. Pulp
- d. Inner enamel epithelium (ameloblasts)
- e. Outer enamel epithelium
- f. Enamel

1

2

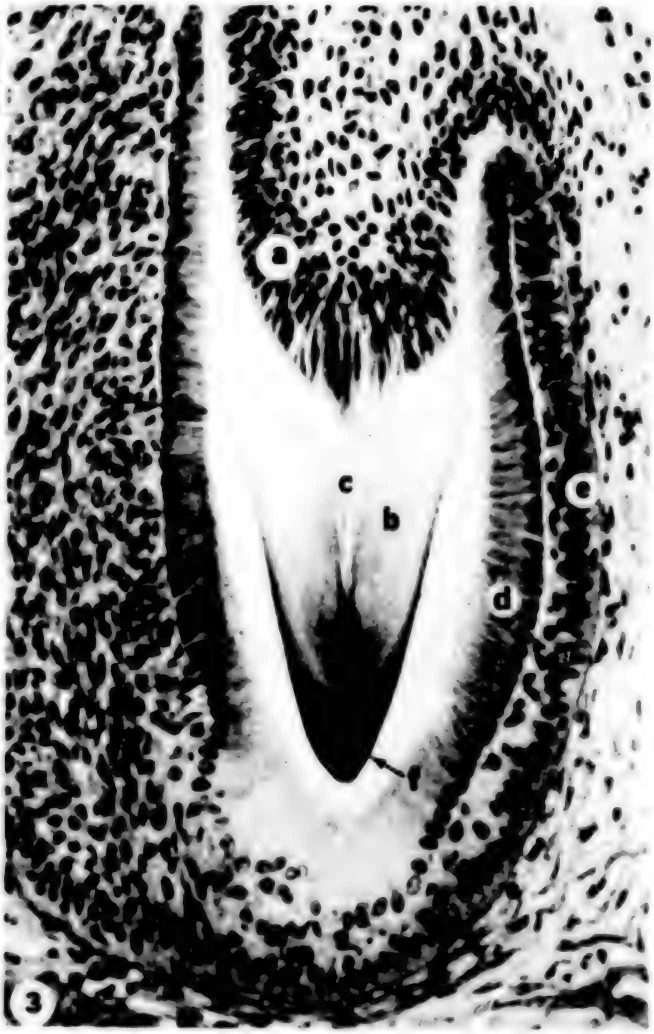


Plate 11. Esophagus

Fig. 1. Longitudinal section of the esophagus of a 1-month-old rainbow trout. × 100.

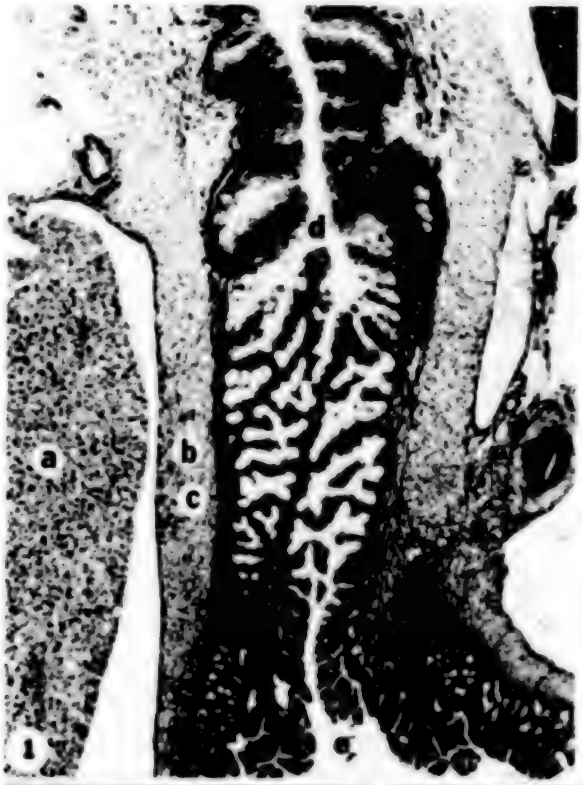
a. Liver
b. Muscularis of the esophagus
c. Crypt of esophageal mucosa
d. Lumen of esophagus
e. Lumen of cardiac stomach

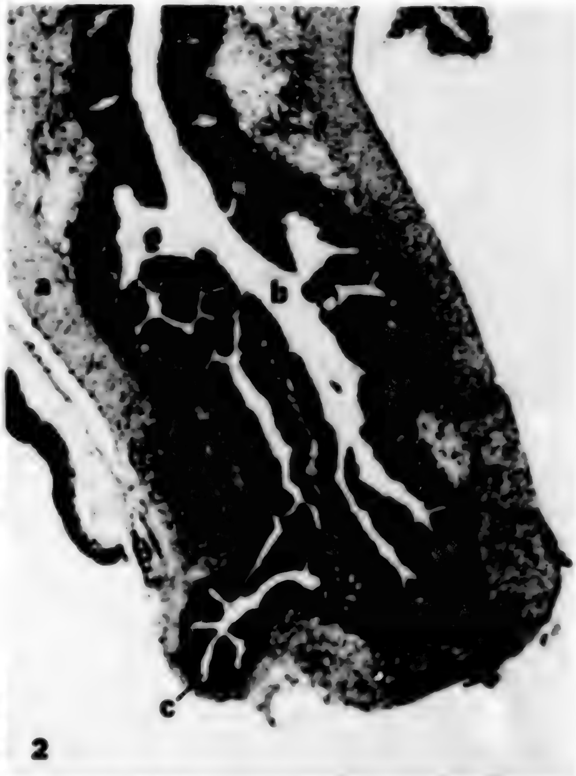
Fig. 2. Longitudinal section of the esophagus at the junction of the pneumatic duct. × 100.

a. Muscularis
b. Lumen of the esophagus
c. Lumen of the pneumatic duct

Fig. 3. Cross section of the posterior portion of the esophagus. × 200.

a. Muscularis longitudinalis
b. Muscularis circularis
c. Submucosa
d. Serous cardiac gland
e. Mucosal fold


1


2

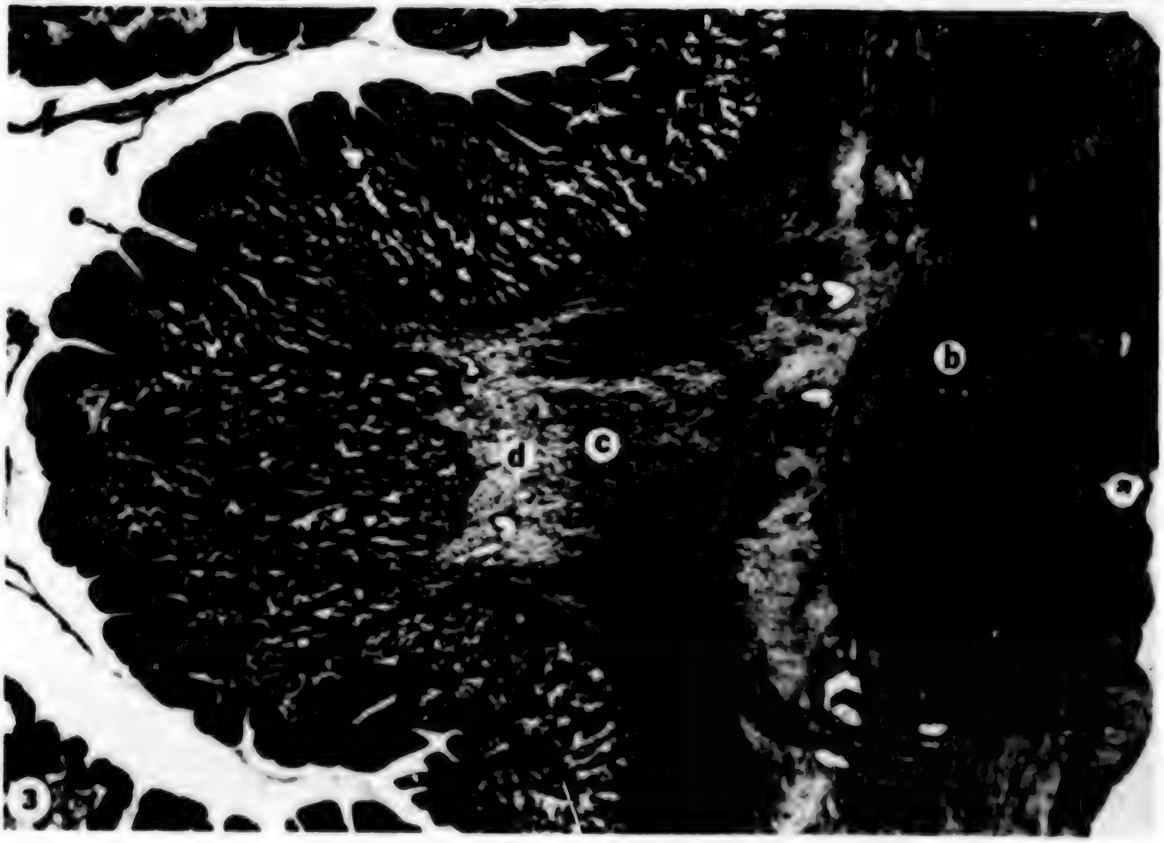

3

Plate 12. Cardiac Stomach

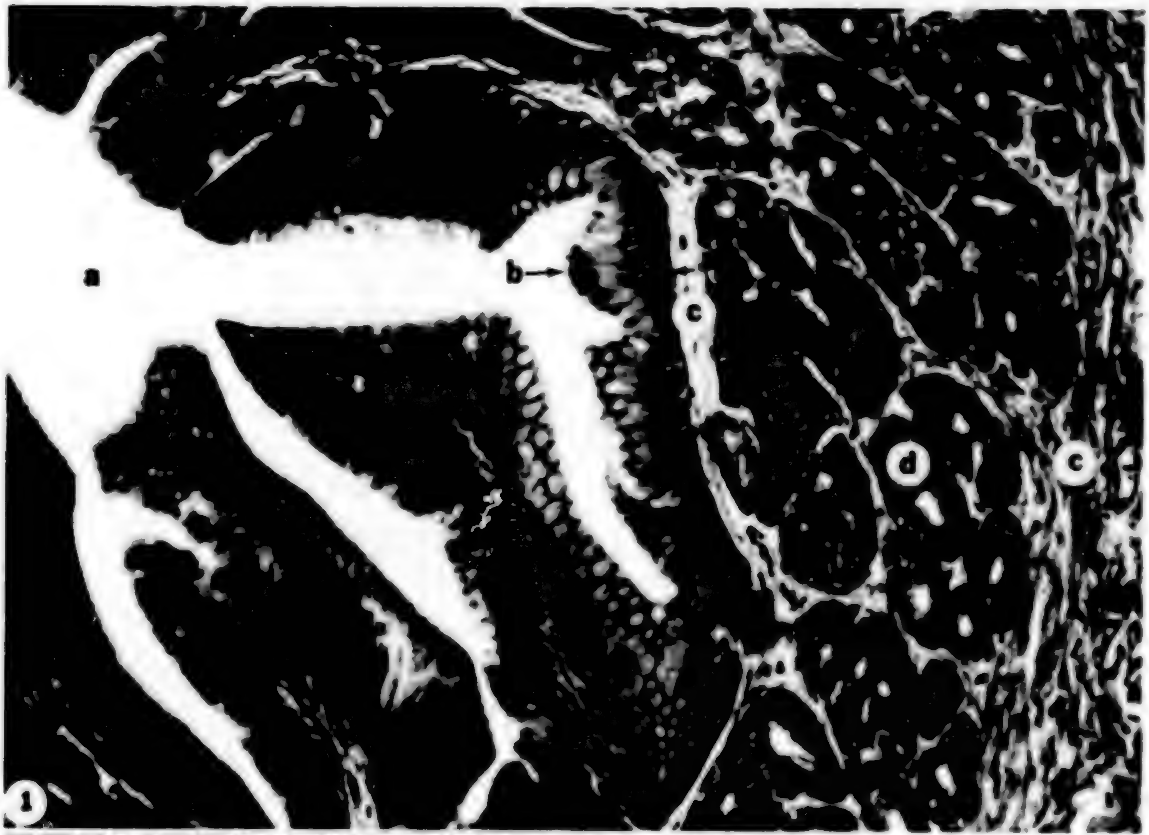
Fig. 1. Cross section of the cardiac stomach of 3-month-old rainbow trout. × 300.

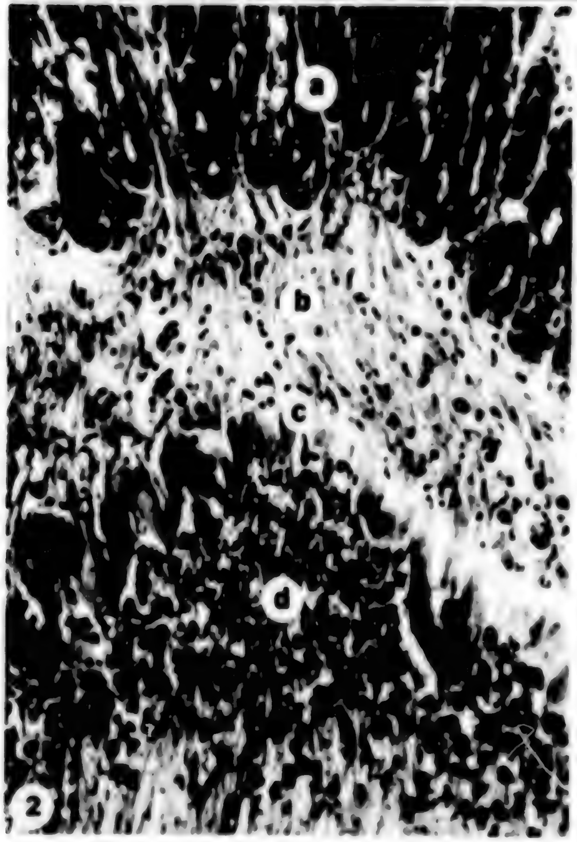
a. Lumen of stomach
b. Columnar cells of the gastric mucosa.
Note the deeply stained wandering lymphocytes at the base of some of these cells (arrow).
c. Connective tissue of the lamina propria, supporting the mucosal folds and cardiac glands.
d. Serous cardiac glands

Fig. 2. Cross section of the cardiac stomach of a yearling rainbow trout. × 200.

a. Serous cardiac glands
b. Lamina propria
c. Stratum compactum
d. Stratum granulosum. The black bodies are clusters of granular cells.

Fig. 3. Details of rectangular portion outlined in Fig. 2 show the individual granules (d). × 500. (Identifying letters [b, c, d] are the same as in Fig. 2.)


a
b
c
d
c
1


a
b
c
d
2

b
c
d
3

Plate 13. Pyloric Stomach (1)

Fig. 1. Cross section of pyloric stomach illustrating the mucosal folds or rugae. × 35.

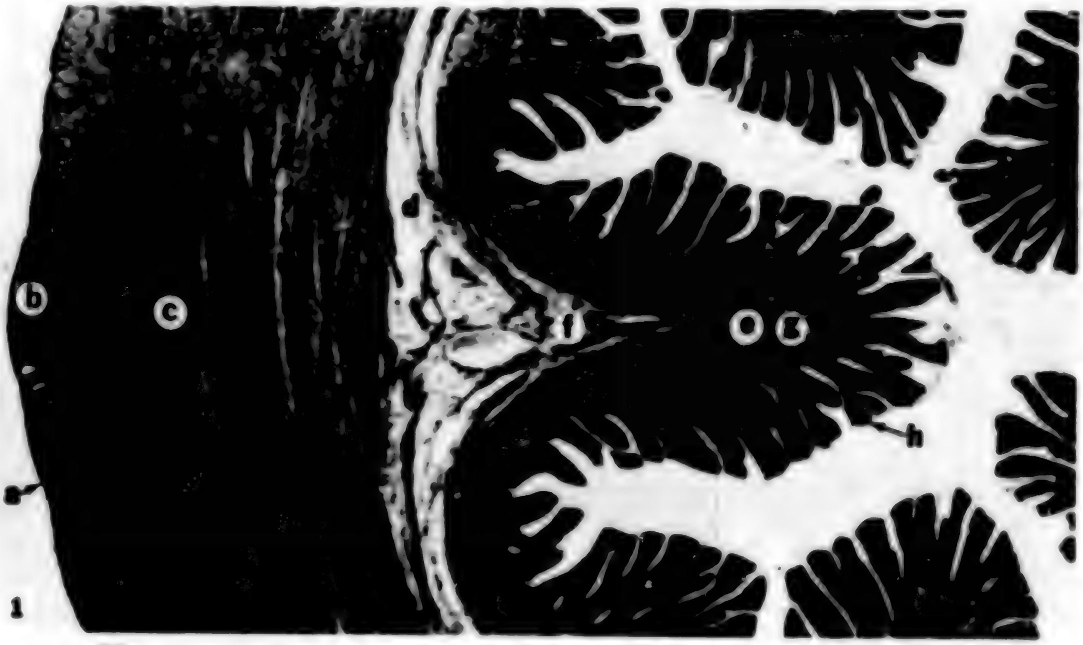
a. Serosa
b. Muscularis longitudinalis
c. Muscularis circularis
d. Submucosa
e. Stratum granulosum
f. Stratum compactum
g. Lamina propria
h. Lamina epithelialis

Fig. 2. Detail of Fig. 1. × 100.

a. Stratum granulosum
b. Stratum compactum
c. Lamina propria
d. Submucosal pit
e. Columnar epithelium

Fig. 3. Detail of upper left central portion of Fig. 2. × 175.

a. Nucleus of epithelial cell
b. Lamina epithelialis


b
c
a
f
h
1

c
d
c
b
2

b
a
3

Plate 14. Pyloric Stomach (2). Sagittal section of the pyloric stomach of a 4-month-old rainbow trout. Masson's trichrome stain. ×625.

a. Serosa
b. Muscularis longitudinalis
c. Muscularis circularis
d. Stratum granulosum
e. Stratum compactum
f. Lamina propria
g. Basement membrane

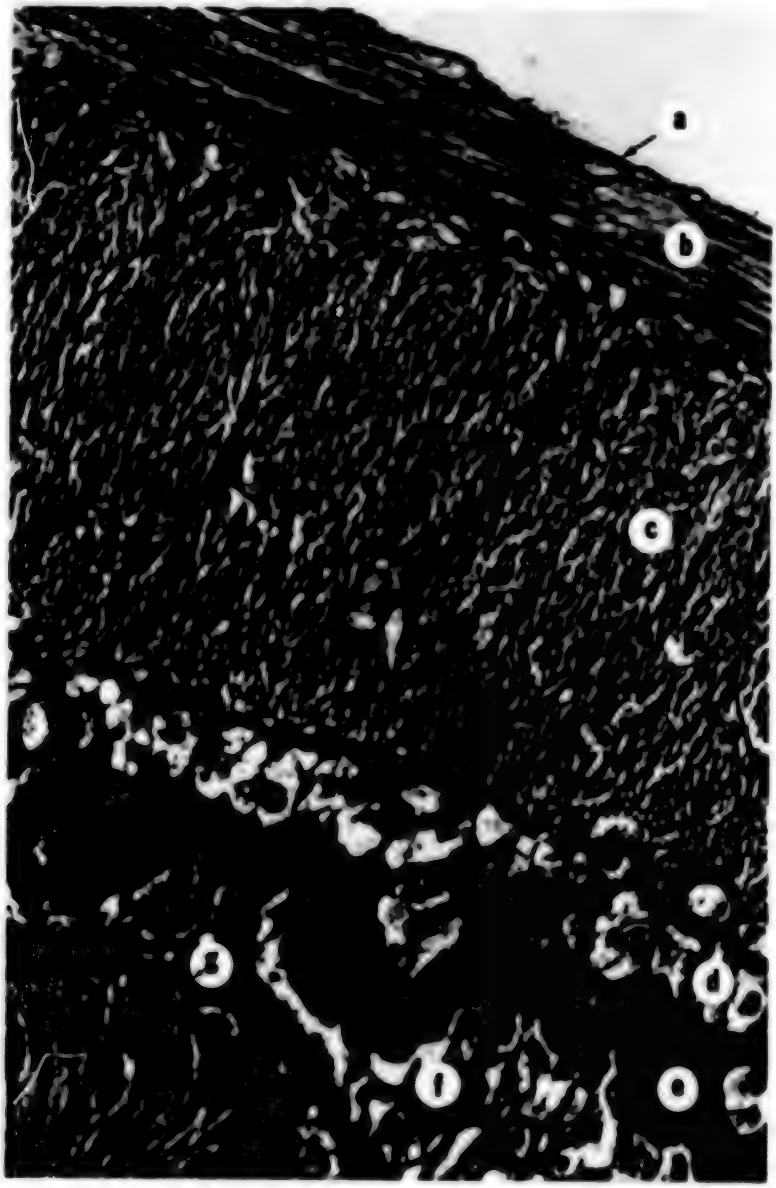

a
b
c
g
d
f
e

Plate 15. Pyloric Caeca

Fig. 1. Longitudinal section through pyloric caeca of a 10-month-old rainbow trout. Note the masses of pancreatic and adipose tissues lying between the caeca. × 30

a. Diffuse pancreatic acinar tissue

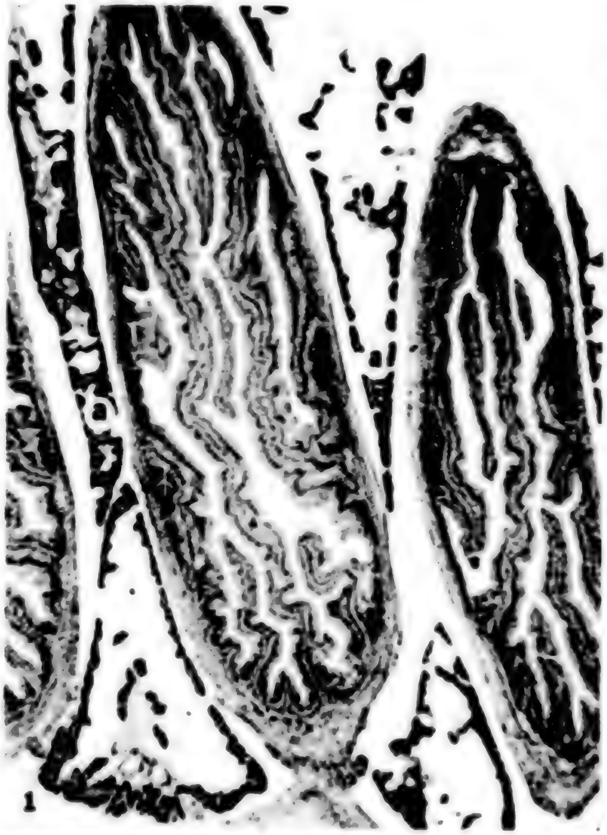
Fig. 2. Cross sections of pyloric caeca surrounded by masses of pancreatic tissue. Note the ducts between the caeca and the pancreatic tissue (arrows, upper left). × 30

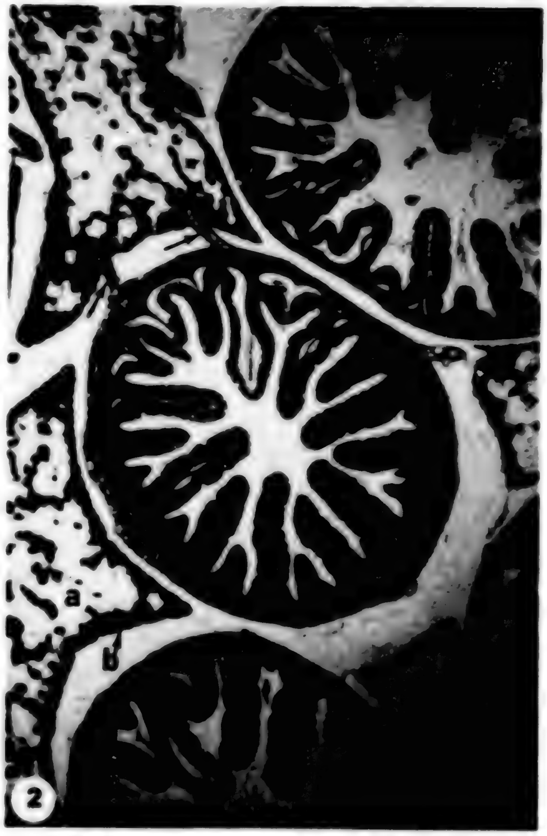
a. Adipose tissue
b. Pancreatic acinar tissue

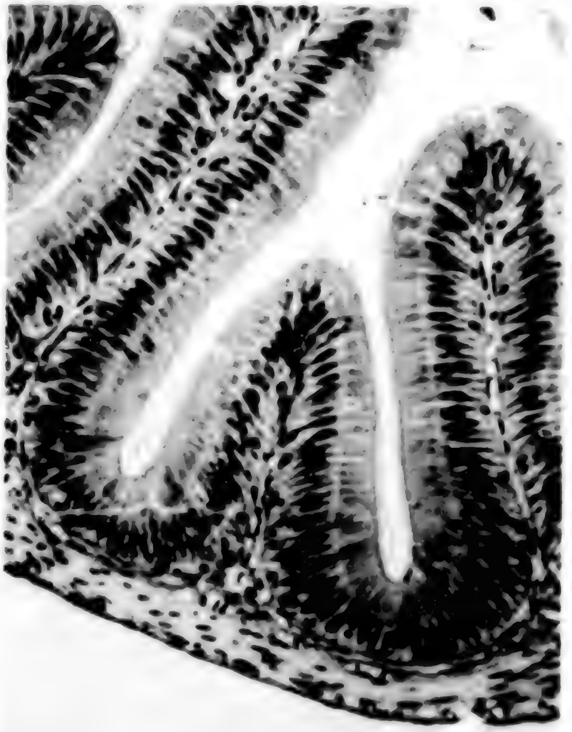
Fig. 3. Detail of pyloric caeca. × 200

Fig. 4. Detail of pyloric caeca. × 600

a. Serosa
b. Muscularis longitudinalis
c. Parasympathetic ganglion cell of Auerbach's plexus
d. Muscularis circularis
e. Stratum compactum
f. Lamina propria
g. Basement membrane
h. Nucleus of columnar epithelial cell
i. Mitotic figure of a dividing epithelial cell
j. Striated border
k. Wandering lymphocyte







3

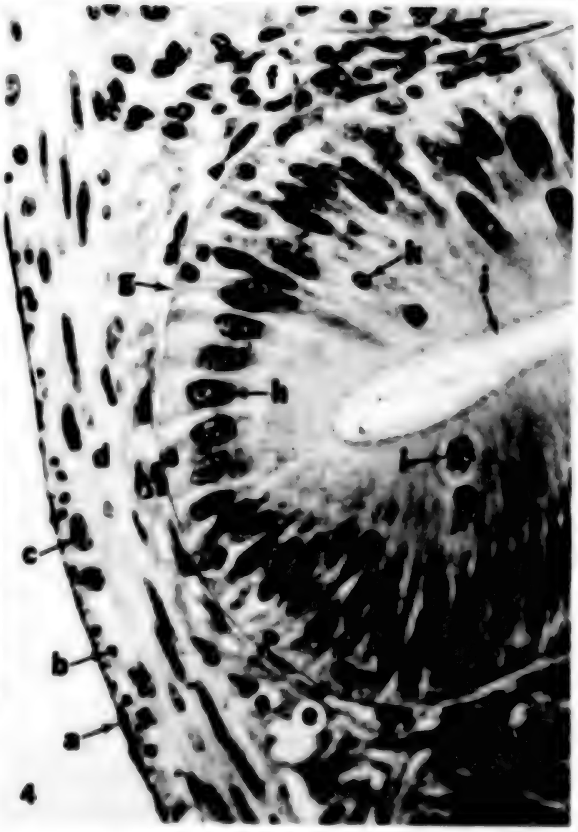
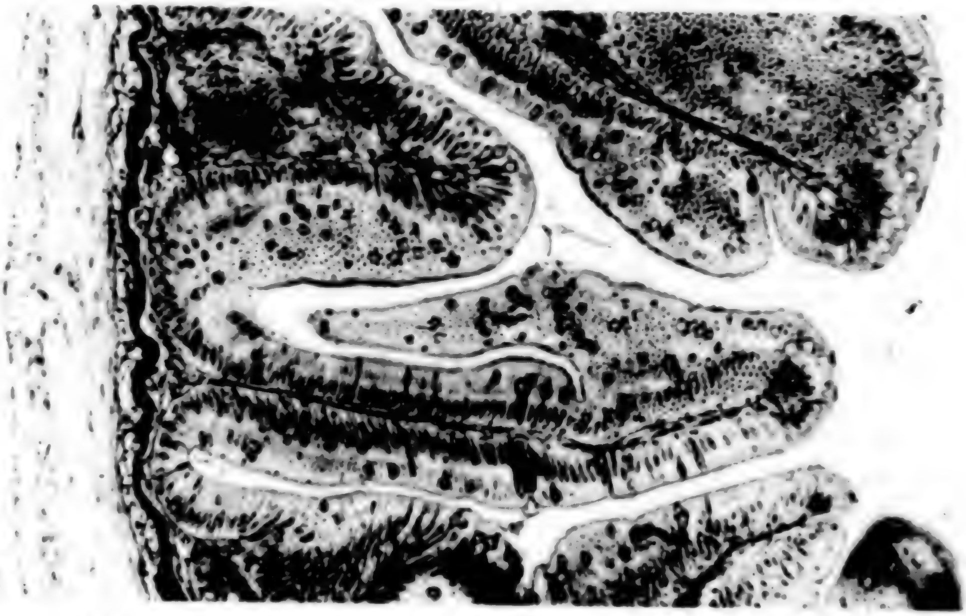


Plate 16. Ascending Intestine (1)

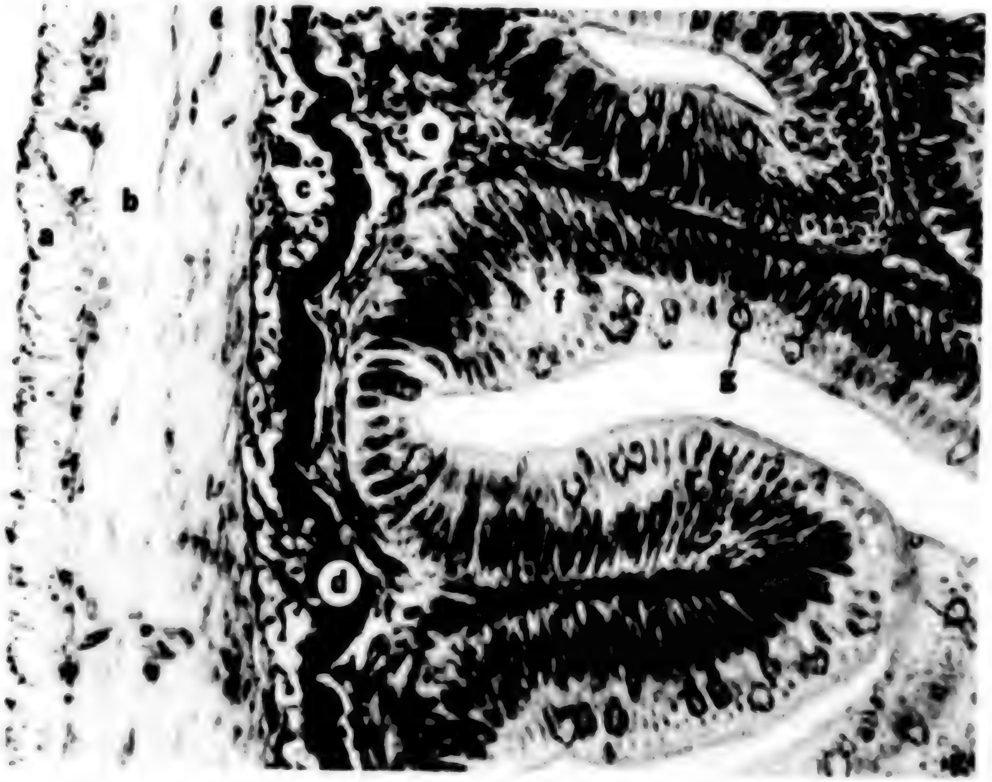
Fig. 1. Detail of a cross section of the ascending intestine of a 3-month-old rainbow trout. × 400.

Fig. 2. Detail of a cross section of the ascending intestine of the same fish. × 1200.

a. Muscularis longitudinalis
b. Muscularis circularis
c. Stratum granulosum
d. Stratum compactum
e. Lamina propria
f. Lamina epithelialis
g. Mucous (goblet) cell



1



2

Plate 17. Ascending Intestine (2). Sagittal section of the pyloric caeca of a 4-month-old rainbow trout. Masson's trichrome stain. × 2100.

a. Serosa
b. Muscularis longitudinalis
c. Muscularis circularis
d. Stratum granulosum
e. Stratum compactum
f. Columnar epithelium
g. Striated border

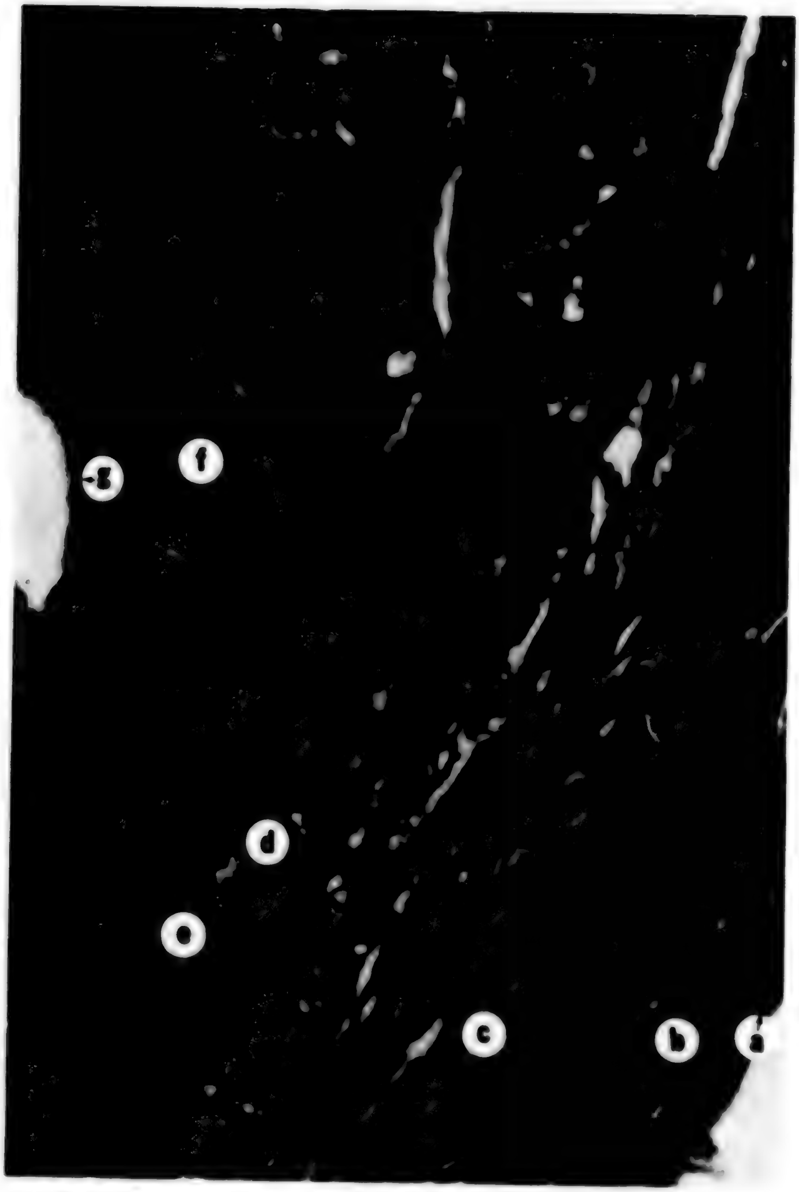

g
f
d
e
c
b
a

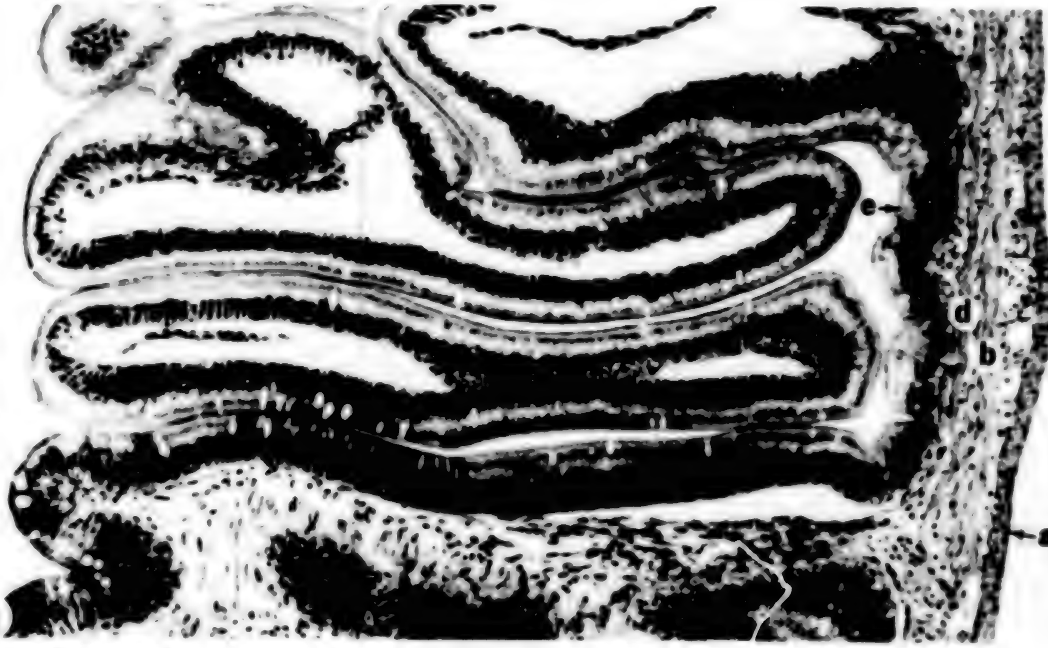
Plate. 18. Descending Intestine

Fig. 1. Detail of a cross section of the descending intestine (posterior intestine or rectum) of a 3-month-old rainbow trout. × 125.

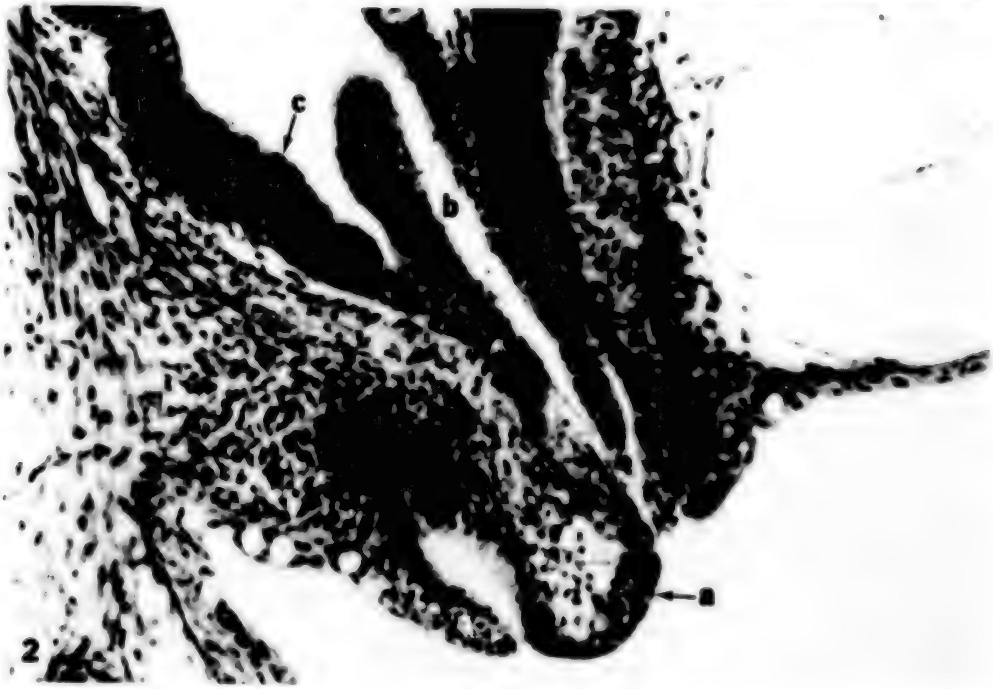
a. Muscularis longitudinalis
b. Muscularis circularis
c. Blood vessel
d. Stratum compactum
e. Lamina epithelialis

Fig. 2. Anal region of a 1-month-old rainbow trout. × 300.

a. Anal papilla
b. Lumen of rectal intestine
c. Lamina epithelialis



1



2

Plate 19. Liver

Fig. 1. Liver of a 3-month-old rainbow trout. × 175.

a. Central vein with erythrocytes
b. Hepatic sinusoid

Fig. 2. Longitudinal section of the anterior body cavity of a 4-month-old rainbow trout. × 15.

a. Liver
b. Lumen of esophagus
c. Ventricle of heart
d. Transverse septum

Fig. 3. Detail of liver parenchyma, showing the characteristic two-cell width of the liver cords. This liver contained few glycogen vacuoles. × 450

Fig. 4. Detail of the liver of a young-of-the-year rainbow trout. Note the abundance of glycogen vacuoles. × 450.

a. Erythrocyte in liver sinusoid
b. von Kupffer cell
c. Glycogen vacuole

Fig. 5. Detail of liver of a young-of-the-year rainbow trout. × 450.

a. Arteriole
b. Bile duct
c. Hepatic sinusoid
d. von Kuppfer cell
e. Nucleus of bile pre-ductule lining cell

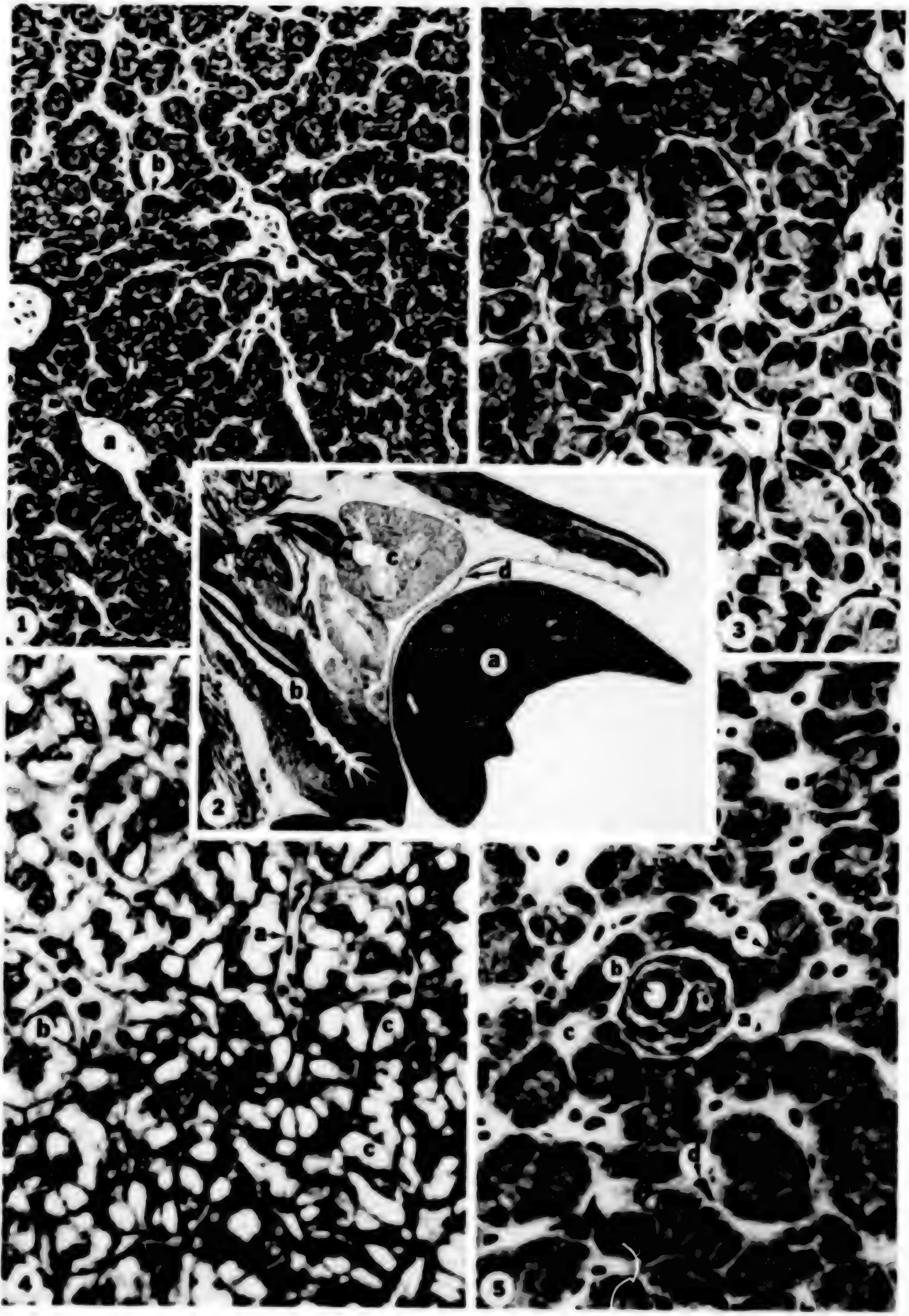

1
b
a
a
2
a
b
c
d
3
4
a
b
c
c
5
b
a
c
d

Plate 20. Biliary Tissue

Fig. 1. Gall bladder of a 3-month-old rainbow trout, in its contracted state. × 40.

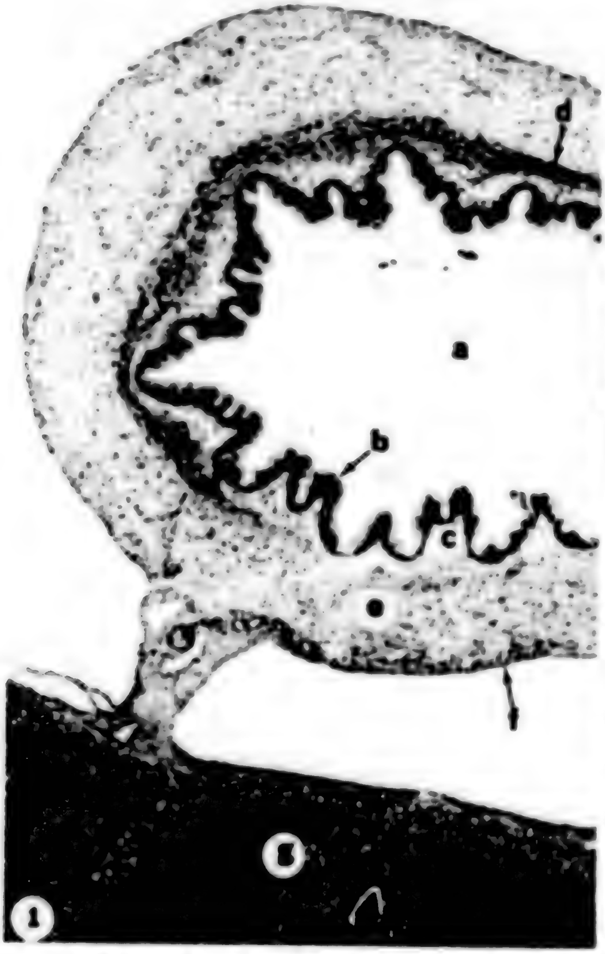
a. Lumen of gall bladder
b. Lamina epithelialis
c. Lamina propria
d. Stratum compactum and stratum granulosum
e. Muscularis
f. Serosa
g. Liver

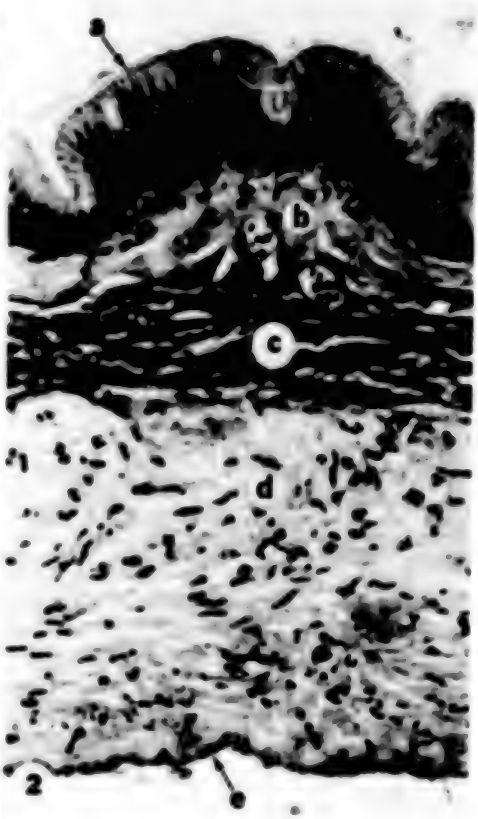
Fig. 2. Detail of Fig. 1. × 100.

a. Lamina epithelialis
b. Lamina propria
c. Stratum compactum and stratum granulosum
d. Muscularis
e. Serosa

Fig. 3. Cross section of ducts within the liver of 3-month-old rainbow trout. × 750.

a. Arteriole, with erythrocytes
b. Nucleus of bile-duct epithelial cell
c. Lumen of bile duct


d
a
b
c
e
f
g
1


a
b
c
d
e
2

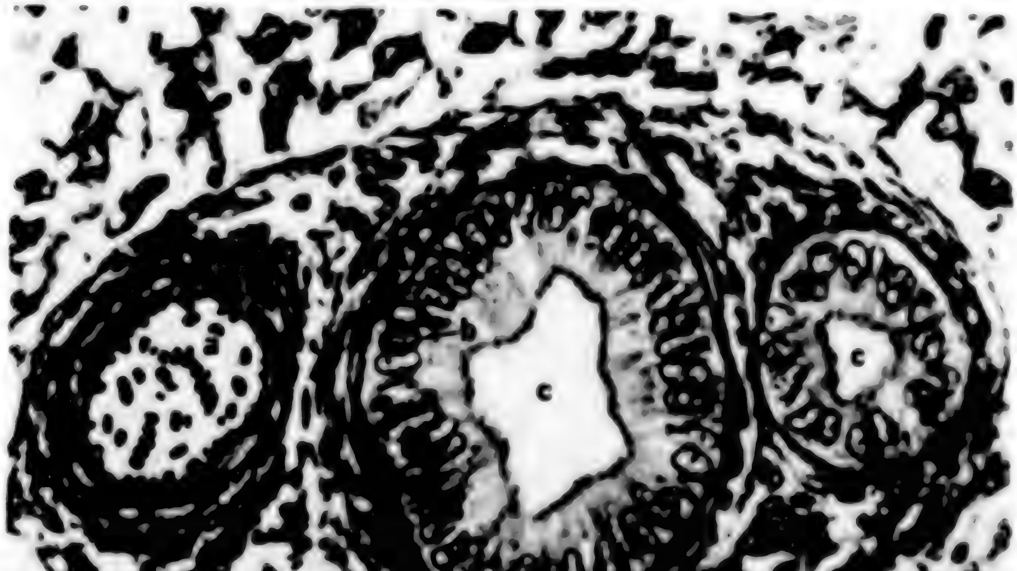

a
b
c
c
3

Plate 21. Pancreatic Tissue

Fig. 1. Mass of pancreatic tissue associated with islet of Langerhans and adipose cells. × 40

a. Pancreatic acini
b. Islet of Langerhans
c. Adipose cells
d. Arteriole
e. Vein with erythrocytes

Fig. 2. Detail of pancreatic acini (dark) and portions of an islet of Langerhans (light). × 800

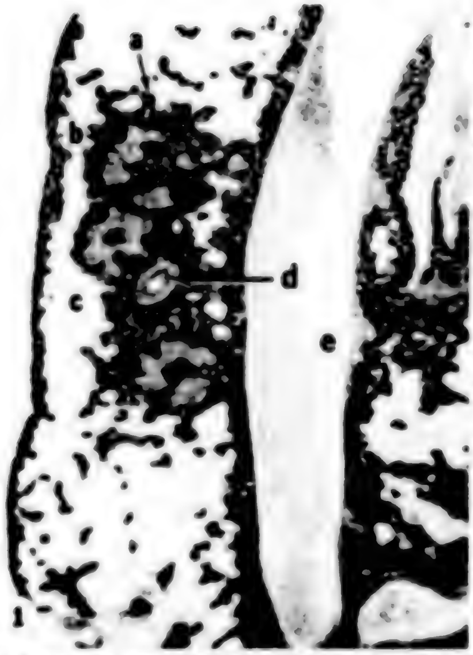
a. Pancreatic acinus
b. Islet of Langerhans

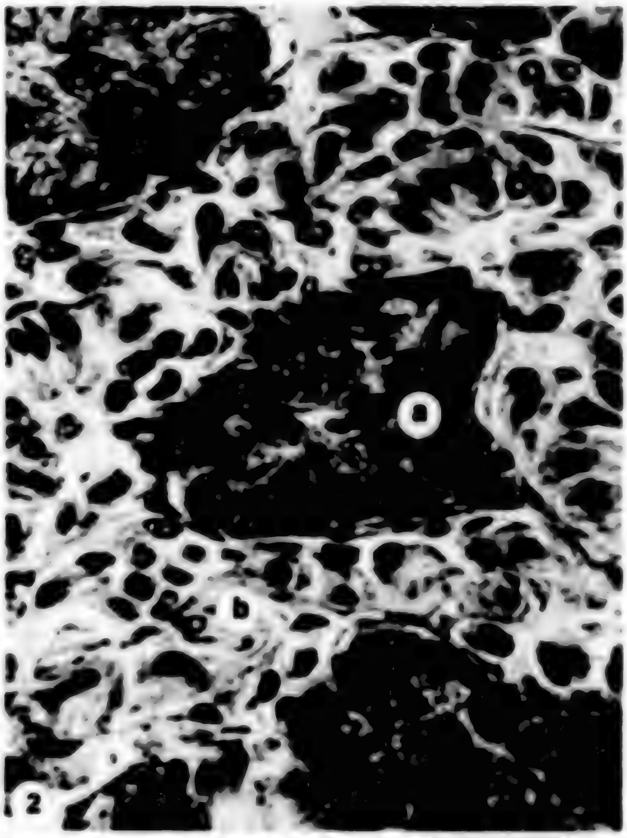
Fig. 3. Pancreatic acinar tissue adjacent to a pyloric caecum. × 675

a. Nucleus of epithelial cell of pyloric caecum
b. Lamina propria
c. Stratum compactum
d. Nucleus of lamina muscularis circularis
e. Nucleus of parasympathetic ganglion cell
f. Nucleus of lamina muscularis longitudinalis cell
g. Serosa
h. Nucleus of centroacinar cell of pancreas
i. Adipose cells, normally occurring with pancreatic tissue
j. Zymogen granules

Fig. 4. Pancreatic acini (dark) and a portion of an islet of Langerhans (light) from a 12-month-old rainbow trout. × 675

a. Islet tissue
b. Acinar cell nucleolus
c. Zymogen granules


a
b
c
d
e
1


a
b
2

a
b
c
d
e
g
h
i
3

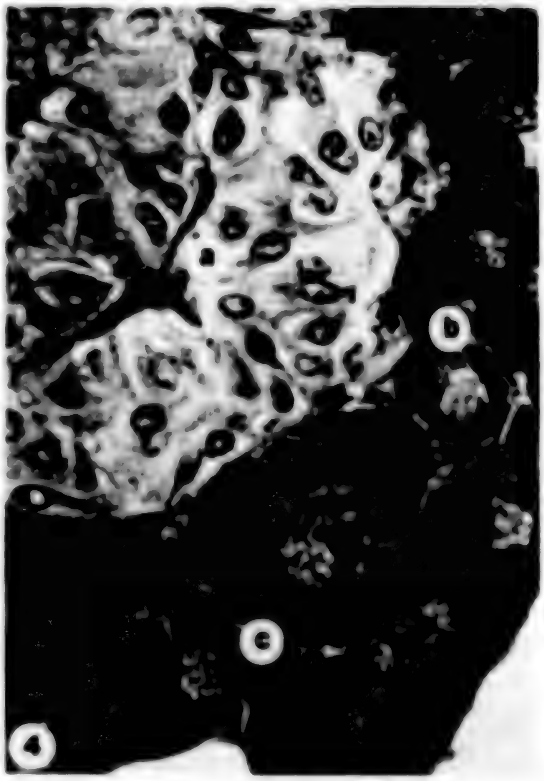

a
b
c
4

Plate 22. Pancreas and Islet of Langerhans. Rainbow trout. 4 months old. May-Grunwold Giemsa stain. × 800.

a A-cells of the islet of Langerhans
b B-cells of the islet of Langerhans
c Pancreatic acinus with cells containing zymogen granules
d Islet of Langerhans
e Pancreatic duct

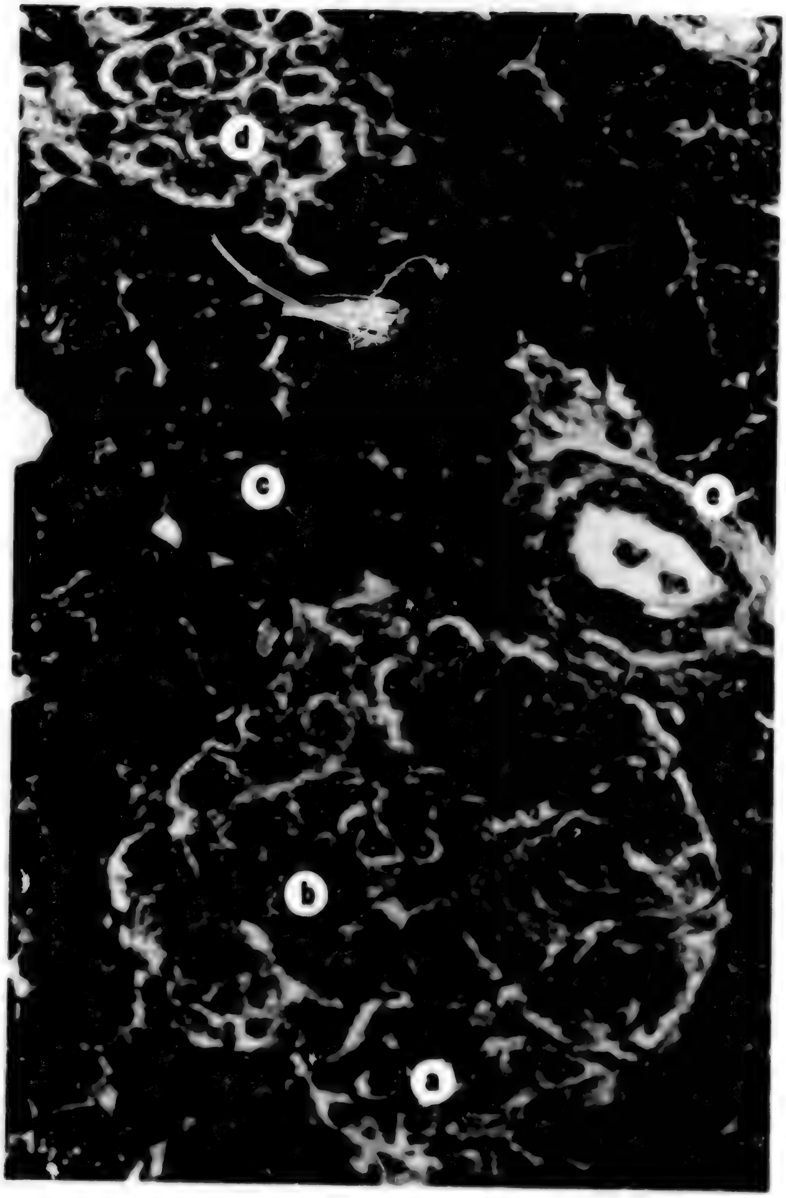

d
c
e
b
a

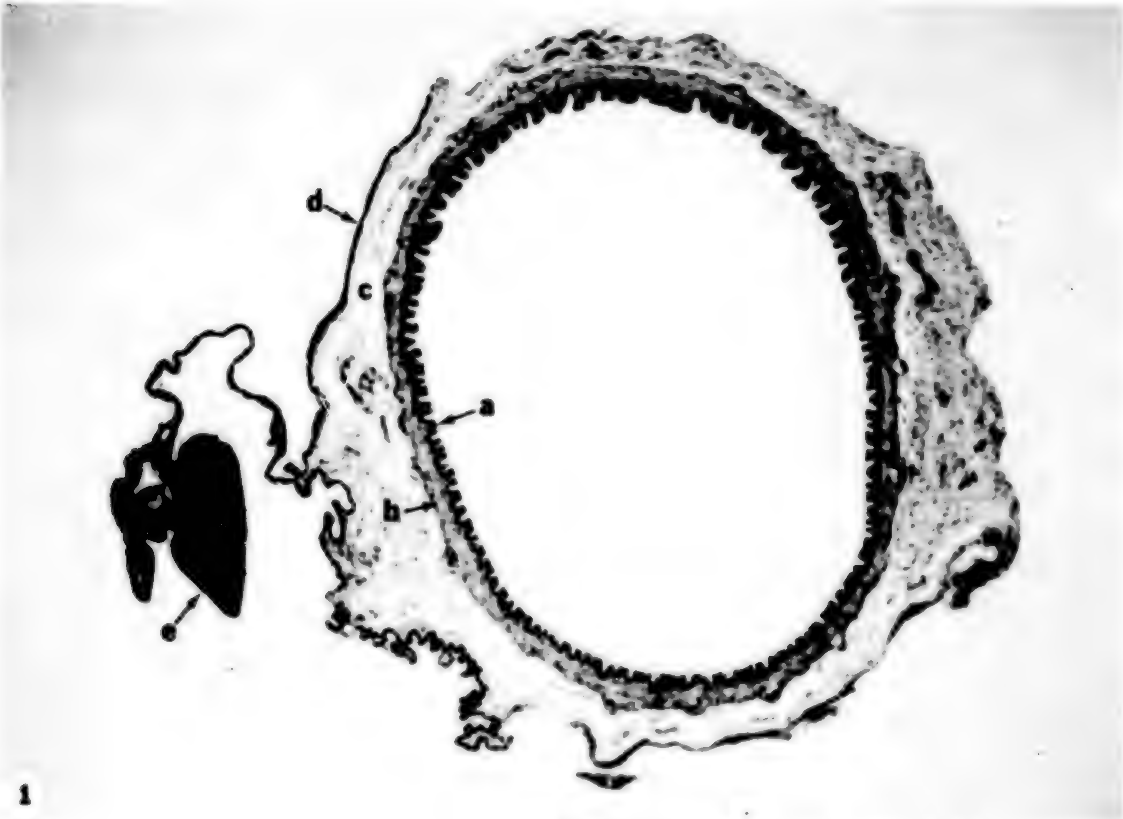
Plate 23. Swim Bladder

Fig. 1. Cross section of the swim bladder of a 6-month-old coho salmon. The fish was relatively small and the bladder was contracted. ×70

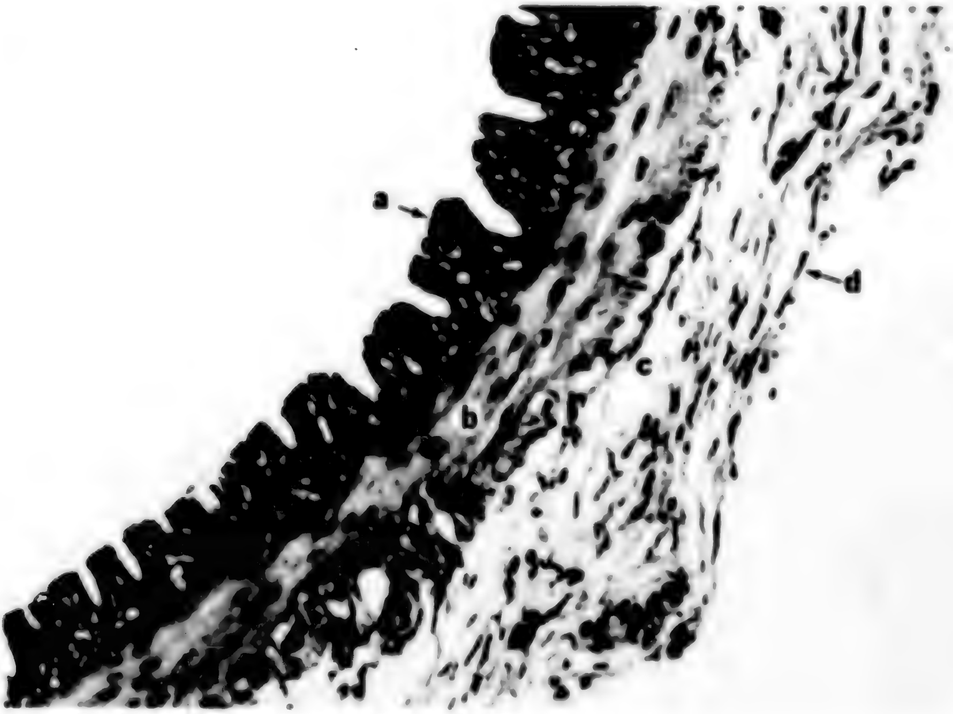
a Lamina epithelialis
b Muscularis
c Connective tissue
d Serosa
e Immature ovary

Fig. 2. Detail of cross section of swim bladder shown in Fig. 1. ×300

a Lamina epithelialis
b Muscularis
c Connective tissue
d Serosa



1



2

Chapter V

Respiratory System

The respiratory tissues of trout are essentially the same as those of most other fishes. Fundamentally the gill is a system for bringing the blood hemaglobin into close contact with the water, so that oxygen can be absorbed and carbon dioxide released. This function necessitates exposure to the water of a system of capillaries with sufficient surface area to effect the required gas exchange. This exposure in turn makes the tissue highly vulnerable to the external environment. Irritation from toxicants, abrasive particles, or parasitic or saprophytic organisms can adversely affect the gill epithelium and reduce respiratory efficiency.

The anatomical structure of the gill is intricate. As shown in Diagram 4, each gill arch has double rolls of paired filaments or primary lamellae. Each filament has a series of lamellae or secondary lamellae located anteriorly and posteriorly, perpendicular to the filament. Detailed gross, microscopic, and ultramicroscopic descriptions of trout gills have been published by a number of investigators (Morgan and Tovell 1973; Olson and Fromm 1973; Cykowska 1978; Hughes 1979; Kendall and Dale 1979; Morrison 1979).

The entire branchial complex is covered with epithelium consisting of unspecialized, dark, chloride and mucous cells (Morgan and Tovell 1973). The so-called unspecialized epithelial cells function as protection and support. The "dark" cells resemble the unspecialized cells, and are scattered uniformly throughout the epithelium of the filaments and lamellae. These two types of cells are not readily seen by light microscopy. Large chloride cells are located along the entire lamellar epithelium but are more numerous at the proximal rather than at the distal end of lamellae (Plate 24). They are more nearly spherical than other epithelial cells and tend to project from the gill surface. Conte (1969) stated that "the name 'chloride' cell is a physiological misnomer because this cell may be involved in the transportation of more than one species of ion." Mucous cells are abundant on the surface of the lamellae, appearing as granule-filled domes or vacuolated cells in light microscopy (Plates 24 and 25). Morrison (1979) described another cell, the "dense" cell, in brook trout, *Salvelinus fontinalis*. These cells are apparently similar to chloride cells, but differ in having a dark cytoplasm; the apical cytoplasm has large round vesicles and large membrane-bound bodies near the nucleus.

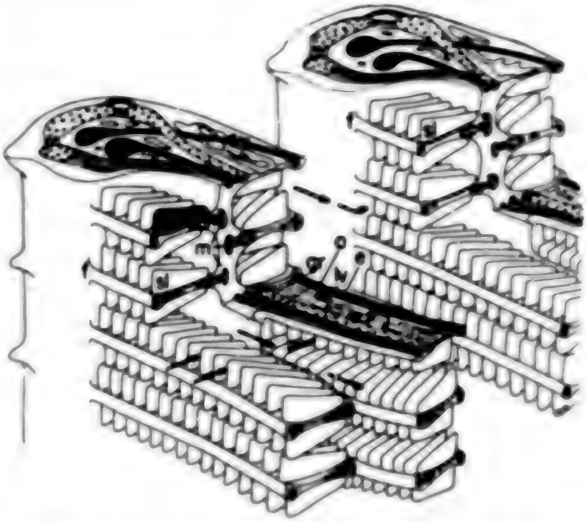


Diagram 4. Schematic diagram of portions of two gill arches of a rainbow trout. Solid arrows show direction of flow of water across the filaments, and broken arrows show direction of blood flow. Abbreviations: gr, gill ray; a, afferent artery; lv, lymph vessel; e, efferent artery; m, muscle bundles; sl, secondary lamella. (Adapted from Morgan and Tovell 1973)

Each lamella is composed of a network of interconnected spaces separated and supported by pilaster (pillar) cells. These spaces are lined with endothelial cells, and these in turn are separated from the double cell layer of epithelial cells by the basement membrane.

Embedded in the superficial tissue of the gill arches are numerous taste buds, supplementing those scattered abundantly throughout the buccal cavity. The gill arches and filaments are supported by a branching system of cartilaginous rods. In addition to the cells and tissues already mentioned, there are two sets of striated muscles – abductor and adductor – which spread the hemibranchs apart or draw them together.

A cluster of gill filaments called the pseudobranch is attached to the underside of each opercle (Plate 25). These filaments are different from the primary respiratory gills in both structure and function. The tissues are the same but the morphology is different (Mattey et al. 1978). In certain respects the pseudobranchs are more "primitive" than the gills; possibly they are less essential and may be termed vestigial. The pseudobranch is apparently the first gill-like structure to develop in the embryo, and probably has an early respiratory function. In the adults of most bony fishes, however, it receives oxygenated blood from the aorta and related vessels and also has a direct vascular connection to the choroid gland of the eye. The pseudobranch, through its production of carbonic anhydrase, is also believed to have a functional relation to the filling of the air bladder (Lagler et al. 1977).

References

Abel, P. D. 1973. An unknown structure in the chloride cells of the gill epithelium of the rainbow trout *Salmo gairdneri*. Z. Zellforsch. Mikrosk. Anat. 146: 293–295.

Abel, P. D. 1976. Toxic action of several lethal concentrations of an anionic detergent on the gills of the brown trout (*Salmo trutta* L.). J. Fish Biol. 9: 441–446.

Adeney, R. J., and G. M. Hughes. 1977. Some observations on the gills of the oceanic sunfish, *Mola mola*. J. Mar. Biol. Assoc. U. K. 57: 825–837.

Bevelander, G. 1935. A comparative study of the branchial epithelium in fishes, with special reference to the extrarenal excretion. J. Morphol. 57: 335–351.

Bierther, M. 1970. Die Chloridzellen des Stichlings. Z. Zellforsch. Mikrosk. Anat. 107: 421–446.

Bijtel, J. H. 1949. The structure and the mechanism of movement of the gill-filaments in Teleostei. Arch. Neerl. 8: 267–288.

Bird, D. J., and A. F. Eble. 1979. Cytology and polysaccharide cytochemistry of the gill of the American eel, *Anguilla rostrata*. Biol. Bull. (Woods Hole) 157: 104–111.

Boland, E. J., and K. R. Olson. 1979. Vascular organization of the catfish gill filament. Cell Tissue Res. 198: 487–500.

Conte, F. P. 1969. Salt excretion. Pages 241–292 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 1. Academic Press, New York.

Conte, F. P., and D. H. Y. Lin. 1967. Kinetics of cellular morphogenesis in gill epithelium during sea water adaptation of *Oncorhynchus* (Walbaum). Comp. Biochem. Physiol. 23: 945–958.

Cooke, I. R. C. 1980. Functional aspects of the morphology and vascular anatomy of the gills of the endeavour dogfish, *Centrophorus scalpratus* (Elasmobranchii: Squalidae). Zoomorphologie 94: 167–184.

Cooke, I. R. C., and G. Campbell. 1980. The vascular anatomy of the gills of the smooth toadfish *Torquigener glaber* (Teleostei: Tetraodontidae). Zoomorphologie 94: 151–166.

Copeland, D. E. 1948. The cytological basis of chloride transfer in the gills of *Fundulus heteroclitus*. J. Morphol. 82: 201–228.

Copeland, D. E., and A. J. Dalton. 1959. An association between mitochondria and the endoplasmic reticulum in cells of the pseudobranch glands of a teleost. J. Biophys. Biochem. Cytol. 5: 393–396.

Cykowska, C. 1978. Changes in microstructure of gills in rainbow trout, *Salmo gairdneri* Richardson, adapted to sea water conditions. Acta Ichthyol. Piscatoria 8: 59–76.

Davis, J. E., and J. N. Cameron. 1971. Water flow and gas exchange at the gills of rainbow trout, *Salmo gairdneri*. J. Exp. Biol. 54: 1–18.

Doyle, W. L. 1961. The so-called chloride cell of the fish gill. Physiol. Zool. 34: 81–85.

Doyle, W. L. 1977. Cytological changes in chloride cells following altered ionic media. J. Exp. Zool. 199: 427–433.

Dunel-Erb, S., and P. Laurent. 1980. Ultrastructure of marine teleost gill epithelia: SEM and TEM study of the chloride cell apical membrane. J. Morphol. 165: 175–186.

Evans, D. H. 1975. Ionic exchange mechanisms in fish gills. Comp. Biochem. Physiol. A. Comp. Physiol. 51: 491–496.

Farrell, A. P. 1980. Vascular pathways in the gill of ling cod, *Ophiodon elongatus*. Can. J. Zool. 58: 796–806.

Fearnhead, E. A., and B. C. Fabian. 1971. The ultrastructure of the gill of *Monodactylus argenteus* (a euryhaline teleost fish) with particular reference to morphological changes associated with changes in salinity. S. Afr. Assoc. Mar. Biol. Res., Oceanogr. Res. Inst., Invest. Rep. 26. 49 pp.

Fishelson, L. 1980. Scanning and transmission electron microscopy of the squamose gill-filament epithelium from fresh- and sea-water adapted *Tilapia*. Environ. Biol. Fishes 5: 161–165.

Fromm, P. O. 1974. Circulation in trout gills: presence of "blebs" in afferent filamental vessels. J. Fish. Res. Board Can. 31: 1793–1796.

Fry, F. E. J. 1957. The aquatic respiration of fish. Pages 1–63 *in* M. E. Brown, ed. The physiology of fishes, vol. 1. Academic Press, New York.

Gannon, B. J., G. Campbell, and D. J. Randall. 1973. Scanning electron microscopy of vascular casts for the study of vessel connections in a complex vascular bed – the trout gills. Annu. Proc. Electron Microsc. Soc. Am. 31: 442–443.

Garcia-Romeu, F., and A. Masoni. 1970. Sur la mise en evidence des cellules a chlorure de la branchie des poissons. Arch. Anat. Microsc. Morphol. Exp. 59: 289–294.

Girard, J. P., and P. Payan. 1980. Ion exchanges through respiratory and chloride cells in freshwater- and seawater-adapted teleosteans. Am. J. Physiol. 7: R260–R268.

Granel, F. 1980. De la pseudobranchie des teleostiens. Bull. Assoc. Anat. 60: 324–330.

Hamada, K. 1967. Specialized cells in the gills of *Chaenogobius castanea* and *Ch. urotaenia*, belonging to the family Gobiidae. Bull. Fac. Fish. Hokkaido Univ. 18: 61–68.

Hamada, K. 1968. Development of a goby, *Chaenogobius urotaenia*, with special reference to the gill and the chloride cell. Bull. Fac. Fish. Hokkaido Univ. 19: 185–197.

Havelka, J., and F. Volf. 1972. Pseudobranchia in fish. Bul. Vysk. Ustav Rybarsky A. Hydrobiolosiky, Vodn. 4: 36–38.

Hoar, W. S. 1924. Development of the swim bladder of fishes. Biol. Bull. (Woods Hole) 47: 79–128.

Hootman, S. R., and C. W. Philpott. 1980. Accessory cells in teleost branchial epithelium. Am. J. Physiol. 7: R199–R208.

Hossler, F. E., J. R. Ruby, and T. D. McIlwain. 1979. The gill arch of the mullet, *Mugil cephalus*. I. Surface ultrastructure. J. Exp. Zool. 208: 379–397.

Hughes, G. M. 1966. The dimensions of fish gills in relation to their function. J. Exp. Biol. 45: 177–195.

Hughes, G. M. 1979. Scanning electron microscopy of the respiratory surfaces of trout gills. J. Zool. (Lond.) 188: 443–453.

Hughes, G. M. 1980. Ultrastructure and morphometry of the gills of *Latimeria chalumnae*, and a comparison with the gills of associated fishes. Proc. R. Soc. Lond. B Biol. Sci. 208: 309–328.

Hughes, G. M., and A. V. Grimstone. 1965. The fine structure of the secondary lamellae of the gills of *Gadus pollachius*. Q. J. Microsc. Sci. 106: 343–353.

Hughes, G. M., and A. K. Mittal. 1980. Structure of the gills of *Barbus sophor* (Ham), a cyprinid with tertiary lamellae. J. Fish Biol. 16: 461–467.

Hughes, G. M., and M. Morgan. 1973. The structure of fish gills in relation to their respiratory function. Biol. Rev. Camb. Philos. Soc. 48: 419–475.

Hughes, G. M., and S. F. Perry. 1976. Morphometric study of trout gills: a light microscopic method suitable for the evaluation of pollutant action. J. Exp. Biol. 64: 447–460.

Hughes, G. M., H. Tuurala, and A. Soivio. 1978. Regional distribution of blood in the gills of rainbow trout in normoxia and hypoxia: a morphometric study with two fixatives. Ann. Zool. Fenn. 15: 226–234.

Hughes, G. M., and E. R. Weibel. 1972. Similarity of supporting tissue in fish gills and the mammalian reticuloendothelium. J. Ultrastruct. Res. 39: 106–114.

Jones, F. R. H., and N. B. Marshall. 1953. The structure and function of the teleostean swimbladder. Biol. Rev. Camb. Philos. Soc. 28: 16–83.

Kashiwagi, M., and R. Sato. 1969. Studies on the osmoregulation of the chum salmon, *Oncorhynchus keta* (Walbaum). II. Histological observations of the branchial epithelium according to the growth of the fish from hatching. Tohoku J. Agric. Res. 20: 212–221.

Kendall, M. W., and J. E. Dale. 1979. Scanning and transmission electron microscopic observations of rainbow trout (*Salmo gairdneri*) gill. J. Fish. Res. Board Can. 36: 1072–1079.

Kessel, R. G., and H. W. Beams. 1960. An electron microscope study of the mitochondria rich "chloride cells" from the gill filaments of freshwater and sea water adapted *Fundulus heteroclitus*. Biol. Bull. (Woods Hole) 119: 322 (Abstr.)

Kessel, R. G., and H. W. Beams. 1962. Electron microscope studies on the gill filaments of *Fundulus heteroclitus* from sea water and fresh water with special reference to the ultrastructural organization of the "chloride cell." J. Ultrastruct. Res. 6: 77–87.

Keys, A., and E. N. Willmer. 1932. "Chloride secreting cells" in the gills of fishes, with special reference to the common eel. J. Physiol. 76: 368–378.

Kirschner, L. B., L. Greenwald, and M. Sanders. 1974. On the mechanism of sodium extrusion across the irrigated gill of sea water-adapted rainbow trout *Salmo gairdneri*. J. Gen. Physiol. 64: 148–165.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. R. M. Passino. 1977. Ichthyology, 2nd ed. John Wiley & Sons, Inc., New York. 545 pp.

Laurent, P., R. G. DeLaney, and A. P. Fishman. 1978. The vasculature of the gills in the aquatic and aestivating lungfish (*Protopterus aethiopicus*). J. Morphol. 156: 173–208.

Laurent, P., and S. Dunel. 1976. Functional organization of the teleost gill. I. Blood pathways. Acta Zool. (Stockh.) 57: 189–209.

Laurent, P., and S. Dunel. 1978. Relations anatomiques des ionocytes (cellules a chlorure) avex le compartiment veineux branchial: definition de deux types d'epithelium de la branchie des Poissons. C. R. Hebd. Seances Acad. Sci. Ser. D. 286: 1447–1450.

Laurent, P., and S. Dunel. 1980. Morphology of gill epithelia in fish. Am. J. Physiol. 7: R147–R159.

Maetz, J. 1971. Fish gills: mechanisms of salt transfer in freshwater and seawater. Philos. Trans. R. Soc. Lond., Ser. B Biol. Sci. 262: 209–250.

Mattey, D. L., R. Moate, and M. Morgan. 1978. Comparison of "pseudobranch" type and "chloride" type cells in the pseudobranch of marine, freshwater and euryhaline teleosts. J. Fish Biol. 13: 535–542.

Mattey, D. L., and D. E. Wright. 1979. A scanning electron microscopic study of the pseudobranch of two marine teleosts. J. Fish Biol. 19: 331–343.

Morgan, M. 1974*a*. The development of gill arches and gill blood vessels of the rainbow trout, *Salmo gairdneri*. J. Morphol. 142: 351–364.

Morgan, M. 1974*b*. Development of secondary lamellae of the gills of the trout *Salmo gairdneri* (Richardson). Cell Tissue Res. 151: 509–524.

Morgan, M., and P. W. A. Tovell. 1973. The structure of the gill of the trout, *Salmo gairdneri* (Richardson). Z. Zellforsch. Mikrosk. Anat. 142: 147–162.

Morrison, C. M. 1979. A dense cell in the epithelium of the gill lamellae of the brook trout, *Salvelinus fontinalis* (Mitchill). J. Fish Biol. 15: 601–606.

Muir, B. S. 1970. Contributions to the study of blood pathways in teleost gills. Copeia 1970: 19–28.

Munshi, J. S. D. 1964. "Chloride cells" in the gills of freshwater teleosts. Q. J. Microsc. Sci. 105: 79–89.

Nakao, T., and K. Uchinomiya. 1978. A study on the blood vascular system of the lamprey gill filament. Am. J. Anat. 151: 239–264.

Newstead, J. D. 1965. Fine structure of respiratory lamellae of teleost gills. Anat. Rec. 153: 383–393.

Newstead, J. D. 1967. Fine structure of the respiratory lamellae of teleostian gills. Z. Zellforsch. Mikrosk. Anat. 79: 369–428.

Olson, K. R., and P. O. Fromm. 1973. A scanning electron microscopic study of secondary lamellae and chloride cells of rainbow trout, *Salmo gairdneri*. Z. Zellforsch. Mikrosk. Anat. 143: 493–449.

Parry, G. 1959. "Chloride-secretory" cells in the gills of teleosts. Nature (Lond.) 183: 1248–1249.

Parry, G., and F. G. T. Holliday. 1960. An experimental analysis of the functions of the pseudobranch in teleosts. J. Exp. Biol. 37: 344–354.

Peek, W. D., and J. H. Youson. 1979. Ultrastructure of chloride cells in young adults of the anadromous sea lamprey, *Petromyzon marinus* L., in fresh water and during adaptation to sea water. J. Morphol. 160: 143–163.

Petrik, P. 1968. The demonstration of chloride ions in the "chloride cells" of the gills of eels (*Anguilla anguilla* L.) adapted to sea water. Z. Zellforsch. Mikrosk. Anat. 92: 422–427.

Philpott, C. W., and D. E. Copeland. 1963. Fine structure of chloride cells from three species of *Fundulus*. J. Cell Biol. 18: 389–404.

Pisam, M. 1981. Membranous systems in the "chloride cell" of teleostean fish gill; their modifications in response to the salinity of the environment. Anat. Rec. 200: 404–414.

Randall, D. J. 1970. Gas exchange in fish. Pages 253–292 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 4. Academic Press, New York.

Richards, B. D., and P. O. Fromm. 1969. Patterns of blood flow through filaments and lamellae of isolated-perfused rainbow trout (*Salmo gairdneri*) gills. Comp. Biochem. Physiol. 29: 1063–1070.

Salewski, W. 1957. The structure and the vascular system of the pseudobranchia by the rainbow trout *Salmo irideus* Gibbons. Folia Morphol. (Warsaw) 8: 27–33.

Sardet, C. 1980. Freeze fracture of the gill epithelium of euryhaline teleost fish. Am. J. Physiol. 7: R207–R212.

Sargent, J. R., B. J. S. Pirie, A. J. Thomson, and S. G. George. 1978. Structure and function of chloride cells in the gills of *Anguilla anguilla*. Pages 123–134 *in* D. S. McLusky and S. J. Berry, eds. Physiology and behaviour of marine organisms. Pergamon, New York.

Shelton, S. 1970. The regulation of breathing. Pages 293–359 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 4. Academic Press, New York.

Skidmore, J. F., and P. W. A. Tovell. 1972. Toxic effects of zinc sulfate on the gills of rainbow trout. Water Res. 6: 217–230.

Smith, D. G. 1976. The structure and function of the respiratory organs of some lower vertebrates. Ph.D. Thesis. University of Melbourne, Victoria, Australia.

Smith, D. G., and D. W. Johnson. 1977. Oxygen exchange in a simulated trout gill secondary lamella. Am. J. Physiol. 233: R145–R161.

Soivio, A., and G. M. Hughes. 1978. Circulatory changes in secondary lamellae of *Salmo gairdneri* gills in hypoxia and anaesthesia. Ann. Zool. Fenn. 15: 221–225.

Steen, J. B., and A. Kruysse. 1964. The respiratory function of teleostean gills. Comp. Biochem. Physiol. 12: 127–142.

Straus, L. P. 1963. A study of fine structure of the so-called chloride cells of the gill of the guppy *Lebistes reticulatus*. Physiol. Zool. 36: 183–198.

Tamura, E., and Y. Honma. 1973. Histological changes in the organs and tissues of gobiid fishes throughout the life-span. V. Seasonal changes in the branchial organs of the flat-head goby in relation to sexual maturity. Bull. Jpn. Soc. Sci. Fish. 39: 1003–1011.

Threadgold, L. T., and A. H. Houston. 1961. An electron microscope study of the "chloride-secretory cell" of *Salmo salar* L., with reference to plasma-electrolyte regulation. Nature (Lond.) 190: 612–614.

Threadgold, L. T., and A. H. Houston. 1964. An electron microscope study of the "chloride cells" of *Salmo salar* L. Exp. Cell Res. 34: 1–23.

Tovell, P. W., M. Morgan, and G. M. Hughes. 1970. Ultrastructure of trout gills. Pages 601–602 *in* P. Favard, ed. Septieme congres international de Microscopie electronique, Grenoble, vol. 3. Societe Francaise de Microscopie Electronique, Paris.

Vickers, T. 1961. A study of the so-called "chloride-secretory" cells of the gills of teleosts. Q. J. Microsc. Sci. 104: 507–518.

Vogel, W. O. P. 1978. Arteriovenous anastomoses in the afferent region of trout gill filaments (*Salmo gairdneri* Richardson, Teleostei). Zoomorphologie 90: 205–212.

Vogel, W., V. Vogel, and H. Kremers. 1973. New aspects of the intrafilamental vascular system in gills of a euryhaline teleost, *Tilapia mossambica*. Z. Zellforsch. Mikrosk. Anat. 144: 573–583.

Vogel, W., V. Vogel, and W. Schlote. 1974. Ultrastructural study of arterio-venous anastomoses in gill filaments of *Tilapia mossambica*. Cell Tissue Res. 155: 491–512.

Vogel, W., V. Vogel, and M. P. Pfautsch. 1976. Arterio-venous anastomoses in rainbow trout gill filaments. A scanning and transmission electron microscope study. Cell Tissue Res. 167: 373–385.

Wood, O. M. 1974. A critical examination of the physical and adrenergic factors affecting blood flow through the gills of the rainbow trout. J. Exp. Biol. 60: 241–265.

Wright, D. E. 1973. The structure of the gills of the elasmobranch, *Scyliorhinus canicula* L. Z. Zellforsch. Mikrosk. Anat. 144: 489–509.

Yousan, J. H., and P. A. Freeman. 1976. Morphology of the gills of larval and parasitic adult sea lamprey, *Petromyzon marinus* L. J. Morphol. 149: 73–103.

Plate 24. Gills

Fig. 1. Several gill filaments sectioned longitudinally through the cartilaginous supporting rods. × 40.

Fig. 2. A distal portion of one of the filaments shown in Fig. 1. × 250.

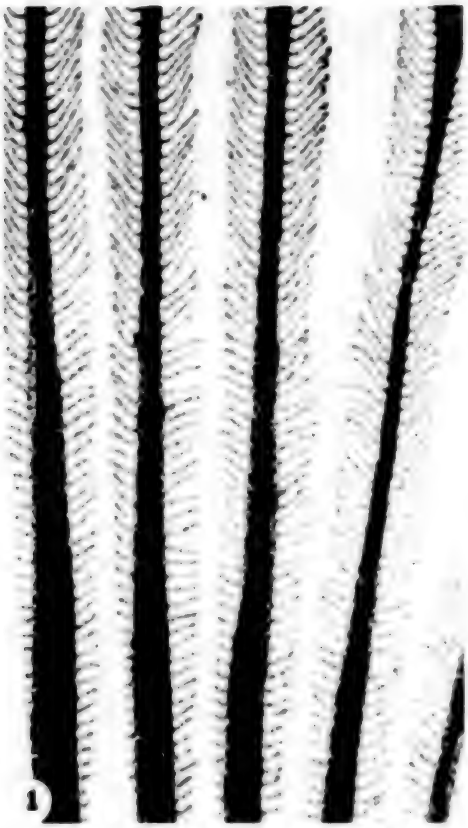
a. Pilaster supporting cell
b. Erythrocyte in lamellar capillary
c. Nucleus of squamous epithelial cell
d. Mucous cell
e. Chloride cells

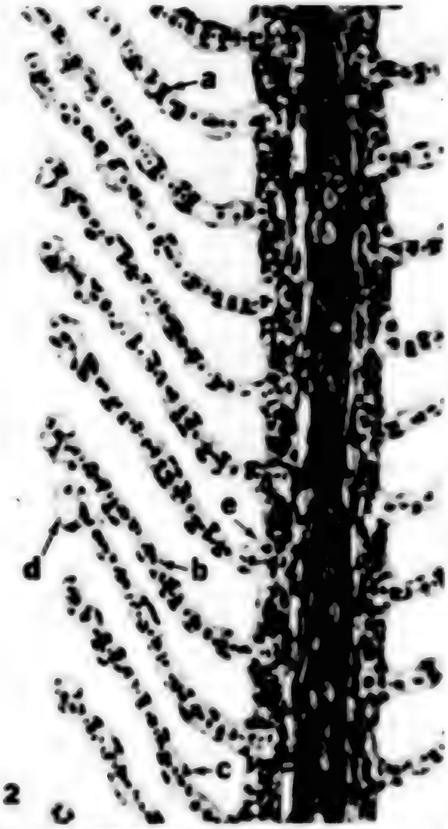
Fig. 3. Detail of filament shown in Fig. 1. × 600.

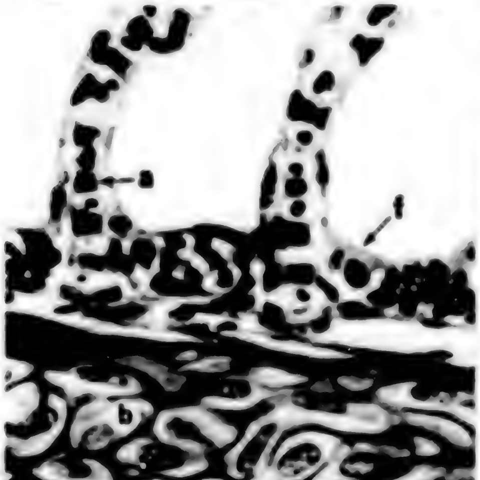
a. Pilaster cell
b. Chondrocyte
c. Mucous cell
d. Nucleus of epithelial cell
e. Two erythrocytes
f. Chloride cell

Fig. 4. Cross section of a gill arch of an 11-month-old rainbow trout, showing the supporting cartilage, blood vessels, and branchial muscle. × 250.

a. Lamella
b. Cartilaginous gill arch
c. Efferent filament artery
d. Afferent filament artery
e. Gill filament muscle


1


a
e
d
b
c
2


a
f
b
d
e
c
3

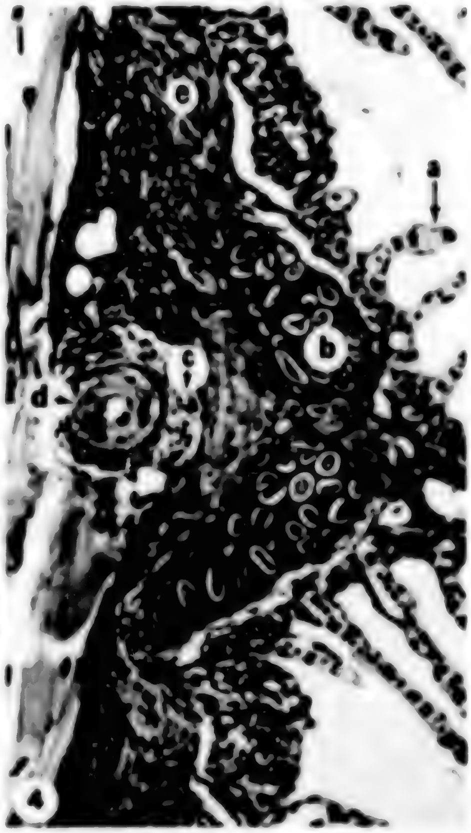

c
a
b
c
d
4

Plate 25. Pseudobranch

Fig. 1. Longitudinal section of the head of a 1-month-old rainbow trout, showing the position of the pseudobranch in relation to other tissues. × 40

a. Pseudobranch
b. Gills
c. Brain
d. Eye
e. Operculum

Fig. 2. Pseudobranch of a 1-month-old rainbow trout similar to that shown in Fig. 1. × 250

Fig. 3. Detail of a pseudobranch of a 9-month-old rainbow trout. × 500

a. Nuclei of the pilaster cells
b. Nuclei of epithelial cells

Fig. 4. Detail of pseudobranch shown in Fig. 2. × 500

a. Portion of the cartilaginous supporting rod
b. Erythrocytes within the afferent vessel
c. Nucleus of epithelial cell
d. Nucleus of pilaster cell
e. Erythrocytes in lamellar capillary

d
c
a
b
1

2

a
b
3

b
d
c
4

Chapter VI

Cardiovascular System

The circulatory system of fish is anatomically simple, compared with that of higher vertebrates. The blood circulates from the heart to the gill arches, where it becomes oxygenated primarily by diffusion through the epithelium of the gill lamellae. It is distributed by way of the dorsal aorta to the arteries and peripheral capillaries and returned to the heart through the venous system. As in most lower vertebrates, the blood flowing through the fish heart is partly unoxygenated. Satchell (1971) gave a comprehensive description of the fish circulatory system. A semi-diagrammatic drawing of the principal features of the salmonid cardiovascular system (from Smith and Bell 1975) reproduced in Plate 26, shows the detailed vascular distribution.

Heart

The heart of trout, like that of all teleosts, is usually described as two chambered; however, it essentially consists of a series of four chambers (Randall 1968, 1970). Blood flows sequentially through four regions: sinus venosus, atrium, ventricle, and bulbus arteriosus (Diagram 5; Plate 26). The walls of these chambers are made of three layers: an inner endocardium, continuous with the arteriovenous system, a medial myocardium; and a peripheral pericardium. The endocardium consists of an endothelium and a subendocardium of loose connective tissue that attaches the endocardium to the myocardium. The myocardium is composed of typical vertebrate cardiac muscle, although the individual muscle fibers are usually smaller in diameter than they are in higher vertebrates (Kilarski 1967). The pericardium consists of two layers: the visceral epicardium, a single layer of mesothelial cells and underlying connective tissue that encloses the heart; and the parietal pericardial sac, in which the heart is suspended.

The sinus venosus is a thin-walled structure that receives venous blood from the hepatic veins and the paired ducts of Cuvier or the common cardinal veins. It is lined internally by endocardium and externally by epicardium, both being one cell thick. The matrix of the sinus venosus wall is composed primarily of connective tissue, plus occasional isolated myocardial cells. The sino-atrial junction does not contain a morphologically distinct pacemaker region, although dense innervation of the region suggests that it functions in this capacity (Santer and Cobb 1972). The sino-atrial valves consist of a cardiac muscle and connective tissue core, lined with endothelium.

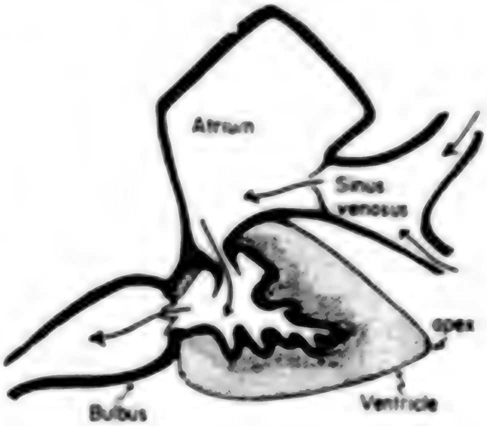


Diagram 5. Trout heart. Arrows show direction of blood flow. (From Randall 1968)

The atrium is also thin-walled but consists of a continuous myocardium sandwiched between the endocardium and the epicardium. Trabeculae, which originate in the outer wall, are also lined with the endocardium (Plate 27, Fig. 1). The atrioventricular valves, which lead into the ventricle, are nonmuscular, connective-tissue structures lined with endocardium.

The heavy-walled ventricle of the trout consists of two layers of myocardium, in addition to the inner endocardium and outer epicardium. A compact cortical or outer layer of muscle lies immediately beneath the epicardium. This layer increases in thickness with increasing age and weight of the fish. The inner trabecular layer has numerous trabeculae, which extend across the ventricular lumen (Plate 27, Fig. 1; Plate 28, Fig. 1). Not all fish have both myocardial layers. Ostadal and Schiefler (1971) concluded that only large, heavy fish have the compact outer layer. Small fish have only the trabecular layer, the basal cells of the trabeculae forming the outer wall of the connective tissue of the ventricle. Ventriculobulbar valves lead from the ventricle into the bulbous arteriosus (Plate 27, Fig. 1).

The fourth heart chamber, the bulbus arteriosus (Plate 27, Fig. 1), is a white, pyriform structure that contains no cardiac muscle. Its walls are made up of elastic connective tissue and smooth muscle. These tissues are arranged into outer circular bundles and inner longitudinal bundles, between which radial bands extend (Plate 28, Figs. 3 and 4).

This arrangement allows for distention and elastic recoil to assist in the propelling of blood anteriorly into the ventral aorta (Priede 1976).

Coronary vessels extend back from the ventral aorta to supply the thick-walled ventricle. They can often be seen in the peripheral epicardium (Plate 27, Fig. 2).

Arteries and Veins

Histologically, the walls of fish arteries and veins, like those of other vertebrates, are composed of three major layers (Plate 29): the intima (inner layer), the media (middle layer), and the adventitia (outer layer). These layers are not always clearly discernible – particularly in veins and small arterioles – because each layer is not always well-developed. The three layers can best be seen in a major elastic or conducting artery such as the ventral aorta. In the ventral aorta (the artery that conducts the blood from the heart to the gills) the intima is thin and composed of an inner endothelium, a medial layer of fibroblasts, collagenous and elastic connective tissue fibers, and the internal elastic membrane. This membrane is composed of two or more elastic layers that are continuous with other elastic fibers in the intima and in the media, and are consequently difficult to see. The media is thick, composing most of the vessel wall. It is composed primarily of circularly arranged elastic fibers, interspersed with smooth muscle cells. The adventitia is thinner than the media and is made up of fibroblasts and collagenous fibers. In contrast, the adventitia of the dorsal aorta is the thickest of the three layers and the intima and media are less well-defined (Satchell 1971). The muscular distributing arteries are smaller than elastic arteries; each of these three layers is also thinner and the media is composed predominantly of smooth muscle fibers, with small amounts of connective tissue. As in higher vertebrates, the distinction between arteries and arterioles is made on the basis of the number of smooth muscle cell layers in the media: three or more layers occur in arteries, and less than three in arterioles.

The three layers that make up the walls of veins are much thinner because they have fewer smooth muscle and elastic components. The intima consists of the endothelium, some collagenous and elastic fibers, and an indistinct internal elastic membrane. Collagenous connective tissue is the predominant tissue of the media as well as of the adventitia. Some smooth muscle cells also occur in the media of medium-sized and large veins. In histologic sections, the endothelium of veins frequently appears somewhat flat because of the sparsity or absence of smooth muscle cells. In arteries, by contrast, the postmortem contraction of smooth muscle cells often throws the elastic membrane into longitudinal folds, causing the entire intima to develop small folds. Thus the internal elastic membrane appears wavy, and the endothelial nuclei are frequently seen projecting into the lumen. The capillaries that distribute blood to the peripheral tissues consist of a single layer of endothelium, facilitating exchanges of oxygen, nutrients, and waste products.

Some teleosts, including the salmonids, have a median ridge – the dorsal aorta ligament – along the dorsal surface of the dorsal aorta (Plate 4, Fig. 1). This elastic longitudinal ligament projects into the lumen of the artery and partly divides it (Satchell 1971). The function of the ligament is still not clear, but Priede (1975) suggested that it can act as a pump during the swimming motion of the fish.

Lymphatic System

Reports by Kampmeier (1970) and Wardle (1971) indicate that much of the information available on the teleost lymphatic system comes from relatively old publications (e.g., Allen 1906; McClure 1915; Burne 1927). Although anatomical aspects of fishes were well documented by Bertin (1958), Lagler et al. (1977), and Kampmeier (1970), no information seems to be available on the detailed histology of the fish lymphatic vessel. Some histological work was reported by Wardle (1971) and Ashley (1975), but these reports mainly delineated additional anatomical features of the system. As in other vertebrates, lymph in fishes is collected from all areas through a system of sinuses and ducts (Plate 30). A lymph heart valve with contractile fibers (like those in heart muscle) can be found in the peduncle area of trout (Lagler et al. 1977).

Histologically, the lymphatic vessels and sinuses in fishes can go unnoticed, because they frequently appear as nearly empty spaces. The walls of the smaller sinuses are extremely thin, and therefore may often be compressed or collapsed in routine tissue sections. The walls of lymphatic vessels are similar to veins and can easily be mistaken for them; however, the lumens of the lymphatics usually contain few or no blood cells (Plate 30, Figs. 2 and 3). Erythrocytes occur more frequently in lymphatic vessels of fish than in those of higher vertebrates (Lagler et al. 1977). Except for the endothelium, the three major layers of the lymphatic vessel wall of fishes are usually difficult to differentiate by light microscopy.

It has recently been suggested that the bilateral lymphatic ducts that lie immediately beneath the dermal layer of the epidermis along the lateral line (Plate 46, Fig. 1; Plate 47) may play an important role in the intake or absorption of various large molecular materials such as vaccines (Amend and Fender 1976).

References

Allen, W. F. 1906. Distribution of the lymphatics in the head, and in the dorsal, pectoral and ventral fins of *Scorpaenichthys marmoratus*. Proc. Wash. Acad. Sci. 8: 41-90.

Amend, D. F., and D. C. Fender. 1976. Uptake of bovine serum albumin by rainbow trout from hyperosmotic solutions: a model for vaccinating fish. Science 192: 793-794.

Anderson, B. C., and D. L. Mitchum. 1974. Atlas of trout histology. Wyo. Game Fish Dep., Bull. 13. 110 pp.

Ashley, L. M. 1975. Comparative fish histology. Pages 3–30 *in* A. E. Ribelin and G. Migaki, eds. The pathology of fishes. University of Wisconsin Press, Madison.

Bell, G. R., and M. J. Smart. 1964. In vivo angiography of the Pacific salmon *Oncorhynchus*. J. Can. Assoc. Radiol. 15: 200–201

Bertin, L. 1958. Appareil circulatoire. Pages 1399–1458 *in* P. P. Grasse, ed. Traite de Zoologie, vol. 13. Mason, Paris.

Burne, N. 1909. Elastic mechanisms in fishes and reptiles. I. Ligamentum longitudinale ventrale of a shad. *Clupea alosa*. Proc. Zool. Soc. Lond. 1909: 201–203

Burne, R. H. 1927. A contribution to the anatomy of the ductless glands and lymphatic system of the angler fish (*Lophius piscatorius*). Philos. Trans. R. Soc. Lond. B. Biol. Sci. 215: 1–56.

DeKock, L. L., and S. Symmons. 1959. A ligament in the dorsal aorta of certain fishes. Nature (Lond.) 184: 194.

Dornesco, G. T., and V. Santa. 1963. La structure des aortes et des vaisseux sanguins de la carpe (*Cyprinus carpio* L.). Anat. Anz. 133: 136–145.

Downey, H. 1909. The lymphatic tissue of the kidney of *Polyodon spathula*. Folia Haematol. (Leipz.) 8: 415–466

Drinker, C. K., and J. M. Yoffey. 1941. Lymphatics, lymph and lymphoid tissue: their physiological and clinical significance. Harvard University Press, Cambridge. 406 pp.

Dunajewski, A. 1930. Die Lymphgefasse im Rumpfe des Aales (*Anguilla anguilla* L.). Bull. Int. Acad. Pol. Sci. Lett. B: 467–478.

Ellis, A. E., and M. de Sousa. 1974. Phylogeny of the lymphoid system. I. A study of the fate of circulating lymphocytes in plaice. Eur. J. Immunol. 4: 338–343

Ferguson, H. W. 1975. Phagocytosis by the endocardial lining cells of atrium of plaice (*Pleuronectes platessa*). J. Comp. Pathol. 85: 561–569

Franz, K. 1897. Uber die Enwicklung von Hypochorda und Ligamentum longitudinale ventrale bei Teleostiern. Morphol. Jb. 25: 143–155.

Good, R. A., J. Finstad, B. Pollara, and A. E. Gabrielsen. 1966. Morphologic studies on the evolution of the lymphoid tissues among the lower vertebrates. Pages 149–170 (Part 3, Chapt. 15) *in* R. T. Smith, P. A. Miescher, and R. A. Good, eds. Phylogeny of immunity. University of Florida Press, Gainesville.

Gorkiewicz, G. 1948. Les Vaisseaux sanguins des muscles du tronc de la truite (*Salmo irideus* Gibb.). Bull. Acad. Pol. Sci. Lett., Ser. B: Sci. Nat. 2: 241–261

Grodzinski, Z. 1946. The main vessels of the brain in rainbow trout (*Salmo irideus* Gibb.). Bull. Acad. Pol. Sci. Lett., Ser. B: Sci. Nat. 2: 1–21

Jensen, D. 1965. The aneural heart of the hagfish. Ann. N.Y. Acad. Sci. 127: 433–458

Johansen, K., and D. Hanson. 1967. Hepatic vein sphincters in elasmobranchs and their significance in controlling hepatic blood flow. J. Exp. Biol. 46: 195–203

Jordan, H. E. 1927. The reticulo-endothelial system with special reference to the lymphocyte. Va. Med. Mon. 53: 776–782

Kampmeier, O. F. 1970. Lymphatic system of the bony fishes. Pages 232–265 *in* Evolution and comparative morphology of the lymphatic system. C. C. Thomas, Springfield, Ill.

Kilarski, W. 1967. The fine structure of striated muscles in teleosts. Z. Zellforsch. Mikrosk. Anat. 79: 562–580

Kisch, B. 1966. The ultrastructure of the myocardium of fishes. Exp. Med. Surg. 24: 220–227.

Kisch, B., and D. E. Philpott. 1963. Electron microscopy of the heart of fish: 1. The goldfish heart. Exp. Med. Surg. 21: 28–53.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. R. M. Passino. 1977. Ichthyology, 2nd ed. John Wiley & Sons, Inc., New York.

Lansing, A. I., F. Lamy, and D. Malkoff. 1960. Connective tissue fibers of the bulbus arteriosus. Anat. Rec. 136: 228–229.

Leak, L. V. 1969. Electron microscopy of cardiac tissue in a primitive vertebrate *Myxine glutinosa*. J. Morphol. 128: 131–158.

Leknes, I. L. 1980. Ultrastructure of atrial endocardium and myocardium in three species of Gadidae (Teleostei). Cell Tissue Res. 210: 1–10.

Leknes, I. L. 1981. The ultrastructure of the atrial myocardial cell in three teleostean species. J. Fish Biol. 18: 81–85.

Leknes, I. L., and T. S. Saetersdal. 1981. On the ultrastructure of specific heart granules in teleosts. J. Fish Biol. 19: 575–579.

Lemanski, L. F., E. P. Fitts, and B. Marx. 1975. Fine structure of the heart in the Japanese medaka, *Oryzias latipes*. J. Ultrastruc. Res. 53: 37–65.

Licht, J. H., and W. S. Harris. 1973. The structure, composition and elastic properties of the teleost bulbus arteriosus in the carp (*Cyprinus carpio*). Comp. Biochem. Physiol. 46A: 699–708.

Martinez-Palomo, A., and R. Mendez. 1971. Presence of gap junctions between cardiac cells in the heart of nonmammalian species. J. Ultrastruct. Res. 37: 592–600.

McClure, C. F. W. 1915. On the provisional arrangement of the embryonic lymphatic system. Anat. Rec. 9: 281–296.

Midttun, B. 1980. Ultrastructure of atrial and ventricular myocardium in the pike *Esox lucius* L. and mackerel *Scomber scombrus* L. (Pisces). Cell Tissue Res. 211: 41–50.

Moore, J. F., W. Mayr, and C. Hougie. 1976. Ultrastructure of coronary arterial changes in spawning Pacific salmon (genus *Oncorhynchus*) and steelhead trout (*Salmo gairdnerii*). J. Comp. Pathol. 86: 259–267.

Muir, B. S. 1970. Contribution to the study of blood pathways in teleost gills. Copeia 1970: 19–28.

Ostadal, B., and T. H. Schiefler. 1971. Uber die terminale Strombahn in Fischherzen. Z. Anat. Entwicklungsgesch. 134: 101–110.

Poupa, O., H. Gesser, S. Jonsson, and L. Sullivan. 1974. Coronary-supplied compact shell of ventricular myocardium in salmonids: growth and enzyme pattern. Comp. Biochem. Physiol. 48A: 85–95

Priede, I. G. 1975. The blood circulatory function of the dorsal aorta ligament in rainbow trout (*Salmo gairdneri*). J. Zool. (Lond.) 175: 39–52.

Priede, I. G. 1976. Functional morphology of the bulbus arteriosus of rainbow trout (*Salmo gairdneri* Richardson). J. Fish Biol. 9: 209–216

Przemyska-Smosarska, J. 1952. Les coeurs lymphatiques chez les Teleosteens. Bull. Int. Acad. Pol. Sci. Lett. B: 77–85

Randall, D. J. 1968. Functional morphology of the heart of fishes. Am. Zool. 8: 179–189

Randall, D. J. 1970. The circulatory system. Pages 133–172 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 4. Academic Press, New York.

Robertson, O. H., B. C. Wexler, and B. F. Miller. 1961. Degenerative changes in the cardiovascular system of the spawning Pacific salmon (*Oncorhynchus tshawytscha*). Circ. Res. 9: 826–834.

Santer, R. M. 1972*a*. An electron microscopical study of the development of the teleost heart. Z. Anat. Entwicklungsgesch. 139: 93–105

Santer, R. M. 1972*b*. Ultrastructural and histochemical studies on the innervation of the heart of a teleost, *Pleuronectes platessa* L. Z. Zellforsch. Mikrosk. Anat. 131: 519–528.

Santer, R. M. 1974. The organization of the sarcoplasmic reticulum in teleost ventricular myocardial cells. Cell Tissue Res. 151: 395–402.

Santer, R. M., and J. L. S. Cobb. 1972. The fine structure of the heart of the teleost, *Pleuronectes platessa* L. Z. Zellforsch. Mikrosk. Anat. 131: 1–14.

Satchell, G. H. 1971. Circulation in fishes. Cambridge monographs in experimental biology, no. 18. Cambridge University Press, London. 131 pp.

Sikorawa, L. 1947. The bordering region of the head and trunk of *Salmo irideus* Gibb. (with special references on its vascular system). Bull. Int. Acad. Pol. Sci. Lett. 1947B11: 299–308.

E COPY

Smith, L. S., and G. R. Bell. 1975. A practical guide to the anatomy and physiology of Pacific salmon. Can. Fish. Mar. Serv. Misc. Spec. Publ. 27. 14 pp.

Sundararaj, B. I., and N. Viswanathan. 1971. Hypothalamo-hypophyseal neurosecretory and vascular systems in the catfish, *Heteropneustes fossilis* (Bloch). J. Comp. Neurol 141: 95–106.

Wardle, C. S. 1971. New observations on the lymph system of the plaice *Pleuronectes platessa* and other teleosts. J. Morphol. Biol. Assoc. U. K. 51: 977–990.

Watson, A. D., and J. I. S. Cobb. 1979. A comparative study on the innervation and the vascularization of the bulbus arteriosus in the teleost fish. Cell Tissue Res. 196: 337–346.

Yamaguchi, A., Y. Fujimaki, and R. Yokota. 1973. Fine structure studies of the sino-auricular nodal tissue in the heart of a teleost fish, *Misgurnus*, with particular reference to the cardiac internuncial cell. Am. J. Anat. 138: 407–429.

Yamauchi, A., and G. Burnstock. 1968. An electron microscopic study on the innervation of the trout heart. J. Comp. Neurol 132: 567–588.

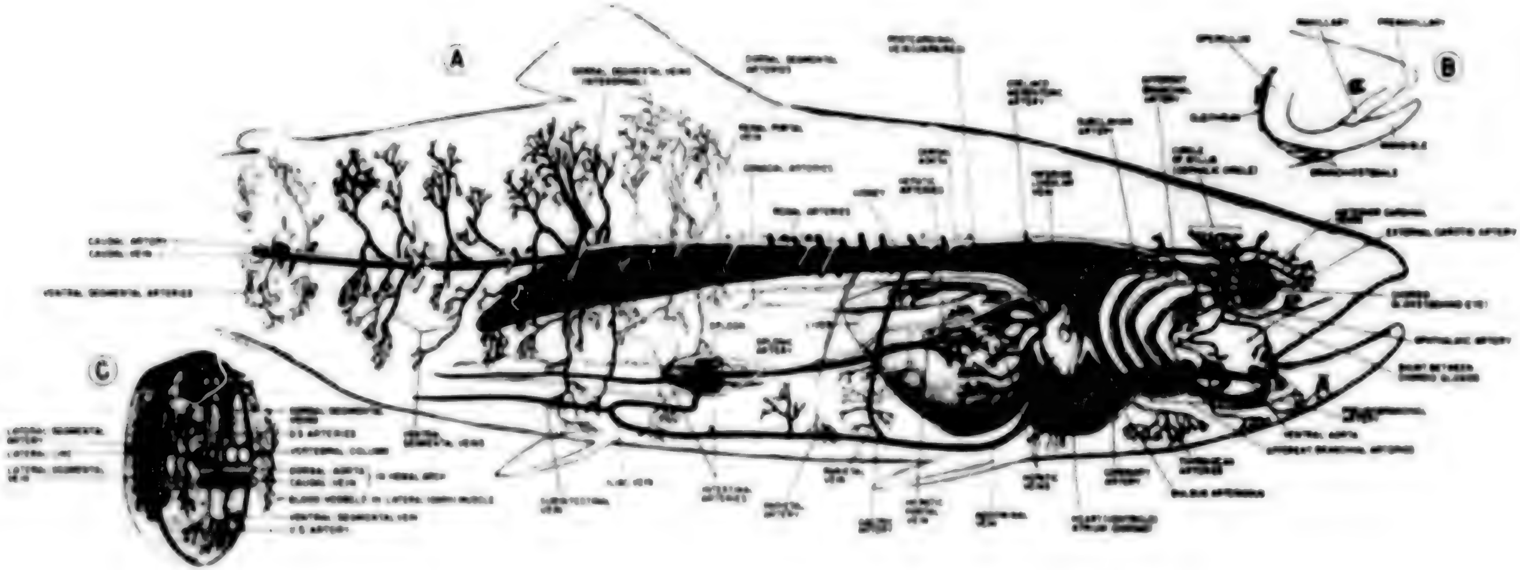
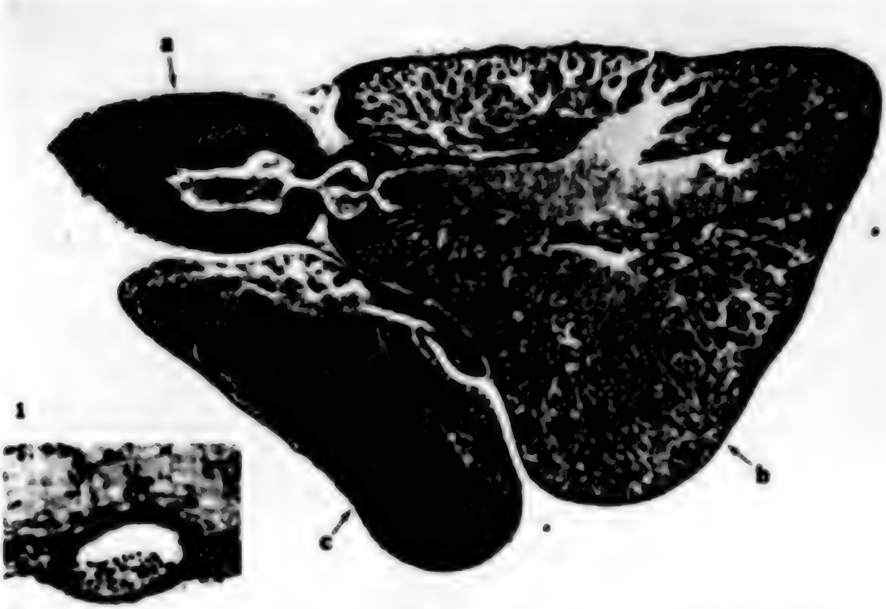
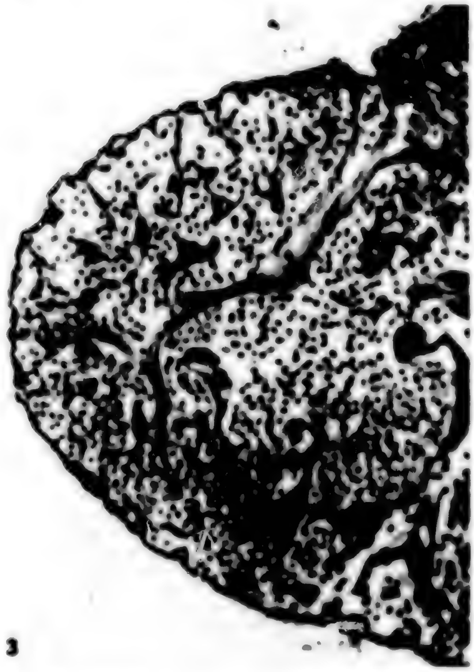


Plate 26. Circulatory System

Semi-diagrammatic drawing of the principal features of the cardiovascular system of a salmonid (A and C) and some external details of the head (B). (From Smith and Bell 1975)

BLANK
PAGE





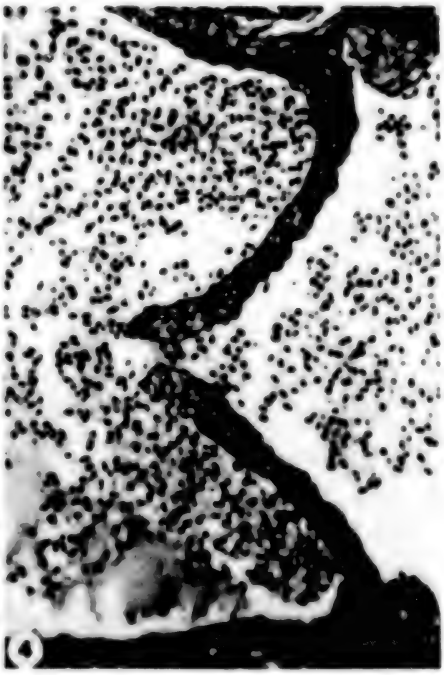


Plate 27. Heart (1)

Fig. 1. Sagittal section of the heart of a 3-month-old rainbow trout. × 50.

- a. Bulbus arteriosus
- b. Ventricle
- c. Atrium

Fig. 2. Detail of coronary artery lying within the visceral epicardium. × 250.

Fig. 3. Detail of ventricle of a yearling rainbow trout, showing the comparatively thick muscular wall)

Fig. 4. Sino-atrial valve of a 3-month-old rainbow trout. × 250.

Plate 28. Heart (2)

Fig. 1. Cardiac muscle fibers from the trabecular layer of the ventricle of a 7-month-old rainbow trout. × 500.

a. Nucleus of muscle fiber
b. Endothelial layer
c. Cardiac muscle striations

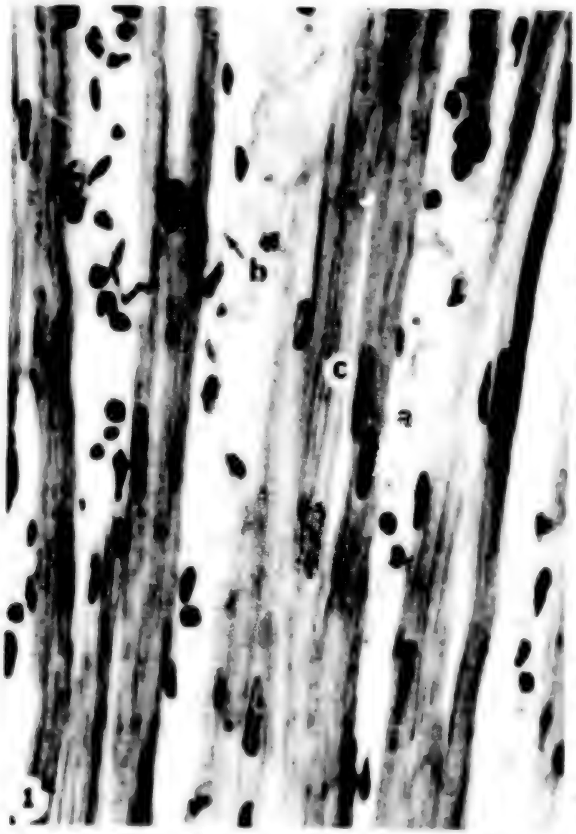
Fig. 2. Cardiac muscle fibers of the atrium of a 4-month-old rainbow trout. × 560

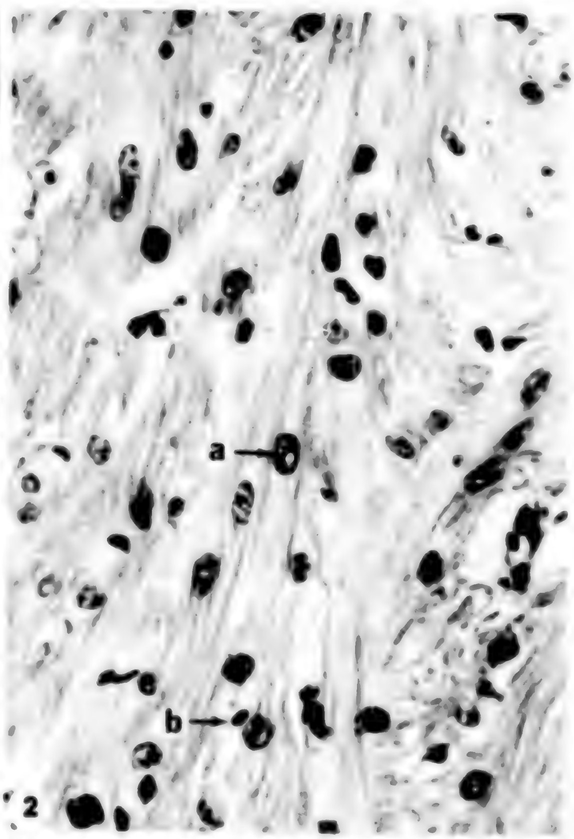
a. Nucleus of muscle fiber
b. Nucleus of red blood cell

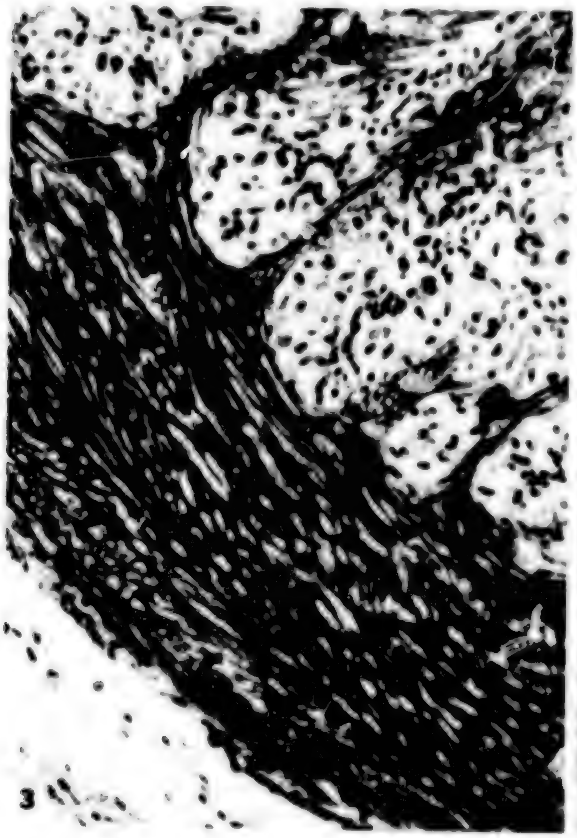
Fig. 3. Cross section of a portion of the bulbus arteriosus. × 250.

Fig. 4. Detail of the bulbus arteriosus. × 560.

a. Nucleus of elastic tissue cell


1


2


3

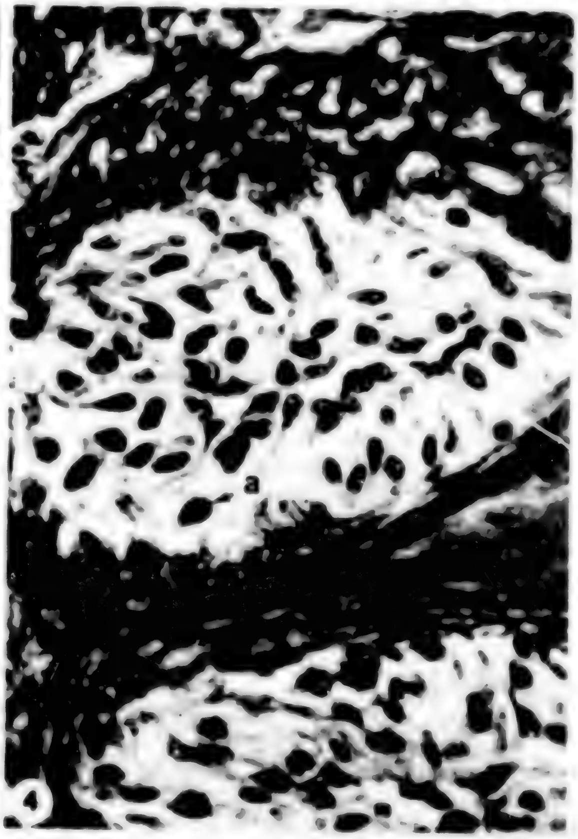

4

Plate 29. Arteries and Veins

Fig. 1. Arterioles and vein in diffuse pancreas. × 500.

a. Pancreatic acinar cells
b. Vein
c. Arterioles

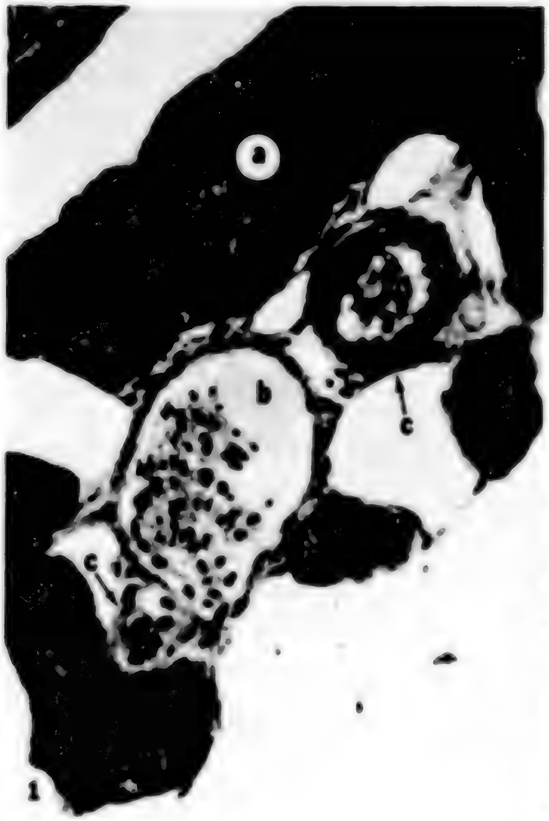
Fig. 2. Hepatic portal triad in liver of 3-month-old rainbow trout. × 700.

a. Hepatic sinusoid
b. Bile duct
c. Venule filled with leucocytes
d. Arteriole

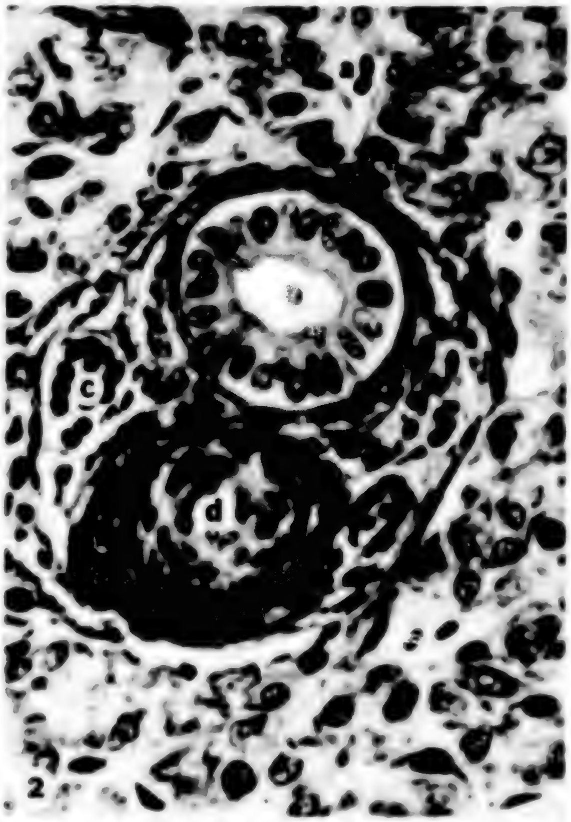
Fig. 3. Vein (filled with erythrocytes) in depot fat. × 250.

Fig. 4. Cross section of the ventral aorta and surrounding thyroid follicles. × 250.

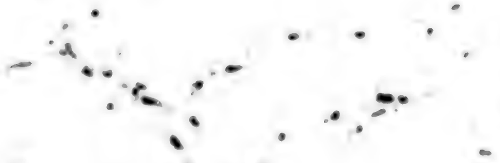
a. Ventral aorta filled with blood cells
b. Thyroid follicles
c. Veins



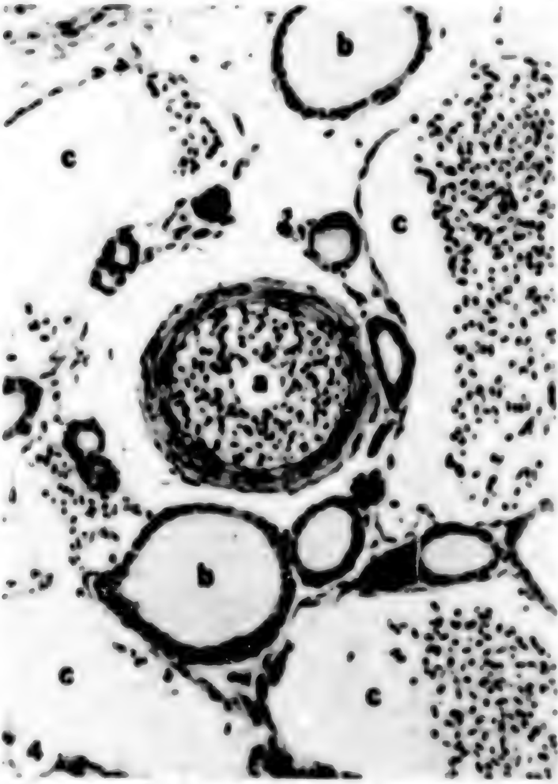
1



2



3



4

Plate 30. Lymphatic System

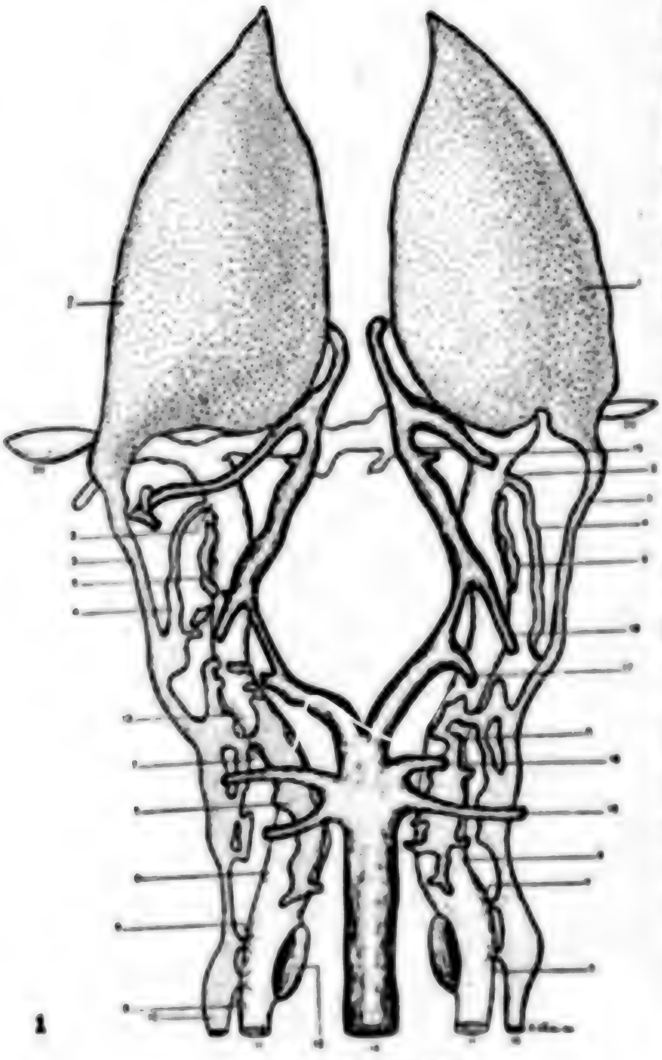
Fig. 1. The lymph, arterial, and venous systems of a rainbow trout embryo, 21 days after egg fertilization. (From McClure 1915)

Fig. 2. Section of the head of a 4-month-old rainbow trout. Dorsal-ventral cross section. × 40

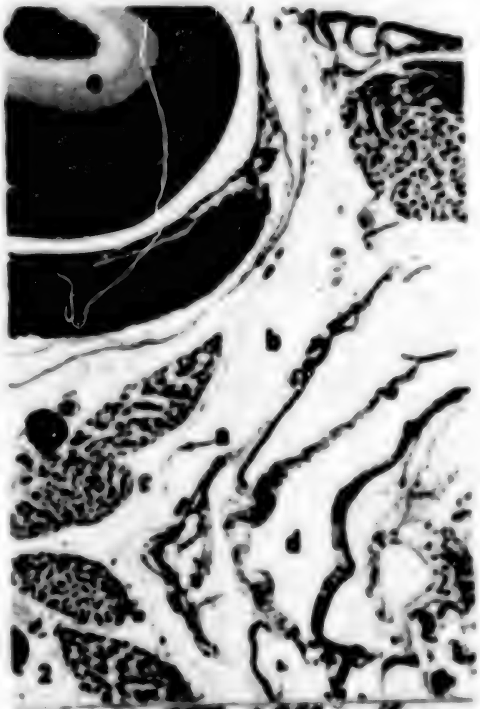
a. Epithelial membrane of the subocular lymphatic sac
b. Lumen of the subocular sac
c. Eye
d. Buccal cavity

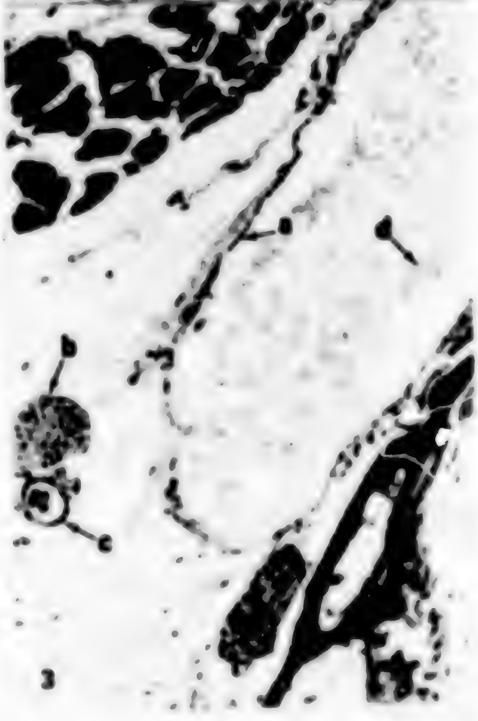
Fig. 3. Detail of portion of Fig. 2. Note the lightly stained film of lymph within the subocular sac. × 200

a. Membrane surrounding the subocular sac (see Fig. 2a)
b. Cross section of nerve
c. Arteriole
d. Film of lymph within the subocular sac



1





REFERENCE NUMBERS

1, Subocular lymph sac
2, Medial pharyngeal communication
3, Lateral pharyngeal lymphatic
4, Medial pharyngeal lymphatic
5, Precardinal (jugular) lymphatic
6, Precardinal (jugular) vein
7, Communication between the precardinal lymphatic and the lateral pharyngeal lymphatic
8, Caudal end of otocyst
9, Cardino-Cuvierian communication
10, Lymphatic of the lateral line of the trunk
11, Postcardinal vein
12, Duct of Cuvier
13, Otic communication
14, Dorsal aorta
15, Hyoidean artery
16, First efferent aortic arch
17, Second efferent aortic arch
18, Third efferent aortic arch
19, Fourth efferent aortic arch
20, Caudal end of eye

Chapter VII

Blood

As in other cold-blooded vertebrates (and in birds), one of the distinctive characteristics of fish blood is the presence of nuclei in mature erythrocytes (red blood cells). Other types of mature cells normally found in peripheral blood of healthy fish are morphologically somewhat similar to human blood cells. One-third to one-half of the total blood volume in fish consists of blood cells (Wedemeyer et al. 1976); the rest is fluid plasma. A peripheral blood smear from a healthy fish shows a preponderance of erythrocytes; other cells are lymphocytes, neutrophils (polymorphonuclear leukocytes), monocytes, and thrombocytes (Plate 31, Figs. 1–4). In healthy young fish up to about 3–4 months old, immature forms of various cell types are frequently present.

The cellular nomenclature used in fish hematology has historically been based on the hematological terminology used in classifying mammalian blood. In recent years several investigators have stressed the importance of considering ontogenic and functional factors, as well as morphological factors, in assigning specific labels to given types of blood cells (Ellis 1976, 1977; MacMillan 1980). Most of the cellular nomenclature used here is based on various interpretations of fish, avian, and mammalian hematologic reports published by numerous other investigators (Catton 1951; Jakowska 1956; Yuki 1957, 1958; Weinreb 1963*a*, 1963*b*; Sekhon and Beams 1969). More recent descriptions of salmonid blood were also considered (Conroy 1972; Klontz 1972; Matsusato 1972; Anderson 1974; Anderson and Mitchum 1974; Lehmann and Sturenberg 1975*b*; MacMillan 1980). An extensive bibliography on fish hematology was published by Hawkins and Mawdesley-Thomas (1972) and an excellent comprehensive review on fish leucocytes by Ellis (1977). All cells described here are from peripheral blood smears prepared without an anticoagulant, and anterior kidney imprints stained with Leischman-Giemsa stain (Wedemeyer and Yasutake 1977), with the exception of one study in which peroxidase stain was used (Yuki 1957, 1958).

Erythrocytes

A mature erythrocyte is an elongated elliptical cell 13–16 µm long by 7–10 µm wide. In Leischman-Giemsa stained smears it has a homogenous pink cytoplasm (Plate 31, Figs. 1–4). The centrally located nucleus is also elliptical, is purplish-red, and has densely compacted chromatin. Polychromatocytes (immature erythrocytes) frequently occur, particularly in healthy fingerling trout (Plate 31, Fig. 3). These cells are usually less elliptical and have a bluish-grey cytoplasm. The nucleus of these cells is not as dense as that of mature erythrocytes. The total red blood cells in young rainbow trout range from 0.77 to 1.58 × 10^6/mm^3 (McCarthy et al. 1973; Wedemeyer and Yasutake 1977). Their primary function is to transport oxygen. In a routine peripheral blood smear, amorphous light-pink bodies are often seen (Plate 31, Fig. 4). These "nuclear shadows" (Yuki 1960) or "ghost" cells (Mulcahy 1970) or "smudge" cells (Conroy 1972) are disintegrated mature red blood cell nuclei, usually considered to be artifacts of techniques used in the preparation of blood smears.

Lymphocytes

Lymphocytes constitute 80 to 98% of the total leucocytes (white blood cells) in juvenile rainbow trout. In smear preparations of peripheral blood, leucocytes are usually sparse among the red blood cells because the normal range in white blood cells is only 7.8 to 20.9 × 10^3/mm^3. Lymphocytes are small spherical cells 7 to 10 µm in diameter. An eccentrically located spherical nucleus, which sometimes has a slight indentation, has fairly compact chromatin and stains reddish-purple. The lightly basophilic narrow band of cytoplasm often has pseudopodial projections (Plate 31, Fig. 2). Cytoplasmic granules are frequently present but are not always visible. Large lymphocytes, 10 to 15 µm in diameter, may also occasionally be seen. These may be immature stages of the small lymphocytes.

Neutrophils (Polymorphonuclear Leukocytes)

The neutrophil is apparently the only granulocytic leukocyte present in rainbow trout (Klontz 1972). Eosinophils and basophils have been reported in other species (Watson et al. 1956, Weinreb 1963*a*, 1963*b*, Conroy 1972; Lester and Desser 1975; Lester and Daniels 1976). Eosinophil-like cells have been reported in rainbow trout hematopoietic tissue by Chiller et al. (1969), and Ellis (1977). We also have frequently observed these cells in the kidney. There are eosinophilic granule cells, commonly called granular cells, in the stratum compactum and stratum granulosum areas of the digestive tract (Plates 14 and 17) that are seriously affected in a salmonid virus disease, infectious hematopoietic necrosis (Yasutake and Amend 1972; Yasutake 1975). Other similar cells referred to as eosinophil granulocytes have been recorded from the fish gill, intestinal tract, and skin (Ellis 1977). The origin or function of these granular cells is not yet known. In many years of examining blood smears and histological sections of normal and diseased salmonids, we have yet to see eosinophils or basophils. Polymorphonuclear leukocytes account for 1 to 9% of the total white blood cells in juvenile rainbow trout. Their diameters are usually slightly larger than those of the smaller lymphocytes, averaging 9 to 13 µm. The nucleus is multi-lobulated (usually it has two to five lobules), and the lobules are frequently connected by thin strands of nuclear material (Plate 31, Fig. 1). Peroxidase stain can be used to differentiate granulocytes from other cells (Yuki 1957), particularly in kidney imprints, where many different stages and types of cells are present (Plate 32, Fig. 4). The role of fish neutrophils in the inflammatory response is still not well understood. They seemingly have a phagocytic function (Finn 1970; Finn and Nielsen 1971; Bell 1976); however, some reports indicate that phagocytosis may not be a primary function (Post 1963; Klontz et al. 1966; Ellis et al. 1976).

Thrombocytes

In salmonid blood smears, as in many other teleost smears, thrombocytes occur in varied shapes: elongated, spiked, fusiform, and spheroid. The elongated form, which has an elliptical dense basophilic nucleus and often has one or two clefts (Plate 31, Fig. 3), is usually not too difficult to distinguish. These cells are about 5–8 µm long – slightly smaller than the small lymphocytes. The very light basophilic cytoplasm, sometimes too lightly stained and therefore difficult to see, may be present as a thin rim around the nucleus. The spike type has streaked cytoplasm on one end, resembling the tail of a comet, whereas the fusiform type has streaks on both ends. The round thrombocytes, with their dense nuclei and little or no cytoplasm, resemble small lymphocytes so closely that the two forms are often indistinguishable. Of the total leukocytes in juvenile rainbow trout, 1 to 6% are thrombocytes (Wedemeyer and Yasutake 1977). Functionally, these cells in fishes are believed to be involved in blood clotting (Srivastava 1969, Wardle 1971) but apparently not in phagocytosis (Ellis 1977), as suggested by some investigators (Yokoyama 1960; Fange 1968). The origin of thrombocytes is still not clear. Some investigators suggest that these cells develop from the same stem cells as the lymphocytes (Catton 1951; Klontz 1972). Others believe that small lymphocytes are the ancestors of the thrombocytes (Gardener and Yevich 1969). From studies conducted on plaice spleen smears, Ellis (1977) hypothesized that the formation tissue of these cells is the spleen.

Monocytes and Macrophages

Ovoid monocytes in peripheral blood are generally large, 9 to 25 µm in diameter (Finn and Nielsen 1971), and are believed to be precursors to macrophages (histocytes). Differentiation of phagocytes usually takes place when they migrate into tissues and become extravascular. Once these cells have migrated into various tissues, they are indistinguishable from macrophages. The cytoplasm of monocytes often has fine granules and takes a moderately basophilic stain. The large nucleus stains like the nuclei of lymphocytes.

Macrophages in fish are frequently found in various tissues and may be readily observed in imprints made from the anterior kidney. They are not usually seen in the circulating system. Phagocytic capability of these cells is well documented (Anderson 1974; Ellis 1976, 1977).

References

Ahaider, H. 1967. Comparative investigations on blood morphology and hematopoiesis of several teleosts. Zool. Anz. 179: 355–409.

Anderson, D. P. 1974. Fish immunology. Book 4 (239 pp.) in S. F. Snieszko and H. R. Axelrod, eds. Diseases of fishes. T. F. H. Publications, Inc. Ltd., Neptune City, New Jersey.

Anderson, B. G., and D. L. Mitchum. 1974. Atlas of trout histology. Wyoming Game Fish Dep. Bull. 13. 110 pp.

Andrew, W. 1965. Comparative hematology. Grune and Stratton, Inc., New York. 188 pp.

Avtalion, R. R., A. Gorlin, E. Gutwirth, and A. Wojdani. 1974. Determination of blood volume in fish: a new method. Bamidgeh 26: 16–20.

Badawi, H. K., and M. M. Said. 1971. A comparative study of the blood of four tilapia species (Pisces). Marine Biol. (Berl.) 8: 202–203.

Barber, D. L., and J. E. M. Westermann. 1975. Morphological and histochemical studies on a PAS-positive granular leukocyte in blood and connective tissues of *Catostomus commersonnii* Lacepède (Teleostei Pisces). Am. J. Anat. 142: 205–220.

Barber, D. L., and J. E. M. Westermann. 1978a. Occurrence of the periodic acid-Schiff positive granular leucocyte (PAS-GL) in some fishes and its significance. J. Fish Biol. 12: 35–43.

Barber, D. L., and J. E. M. Westermann. 1978b. Observations on development and morphological effects of histamine liberator 48/80 on PAS-positive granular leukocytes and heterophils of *Catostomus commersoni*. J. Fish Biol. 13: 563–573.

Barber, D. L., and J. E. M. Westermann. 1981. The blood cells of the Antarctic icefish *Chaenocephalus aceratus* Lonnberg: light and electron microscopic observations. J. Fish Biol. 19: 11–28.

Bell, G. R. 1976. Preliminary observations on phagocytosis in the peripheral blood of sockeye salmon (*Oncorhynchus nerka*). Fish Pathol. 10: 237–241.

Bessis, M. 1973. Living blood cells and their ultrastructure. Springer-Verlag, New York. 767 pp. (Translated from French by R. I. Weed.)

Blaxhall, P. C. 1972. The haematological assessment of the health of freshwater fish. A review of selected literature. J. Fish Biol. 4: 593–604.

Blaxhall, P. C., and K. W. Daisley. 1973. Routine haematological methods for use with fish blood. J. Fish Biol. 5: 771–781.

Buckley, J. A., C. M. Whitmore, and R. I. Matsuda. 1976. Changes in blood chemistry and blood cell morphology in coho salmon (*Oncorhynchus kisutch*) following exposure to sublethal levels of total residual chlorine in municipal wastewater. J. Fish. Res. Board Can. 33: 776–782.

Cannon, M. S., H. H. Mollenhauer, T. E. Eurell, D. H. Lewis, A. M. Cannon, and C. Tompkins. 1980. An ultrastructural study of the leukocytes of the channel catfish, *Ictalurus punctatus*. J. Morphol. 164: 1–23.

Casillas, E. 1974. Stress induced changes in blood coagulation parameters and hematology in a hatchery strain and wild type rainbow trout (*Salmo gairdneri*). M.S. Thesis. University of Washington, Seattle.

Casillas, E., and L. Smith. 1977. Effect of stress on blood coagulation and haematology in rainbow trout (*Salmo gairdneri*). J. Fish Biol. 10: 481-491.

Catton, W. T. 1951. Blood formation in certain teleost fishes. Blood 6: 39-60.

Cavicchioli, G., and A. Zavarini. 1977. Observations on the morphology and seasonal variations of blood cells in the whitefish bondella, *Coregonus macrophthalmus* Nussl. of Lake Maggiore (North Italy). Monit. Zool. Ital. (N.S.) 11: 173-182.

Chiller, J. M., H. O. Hodgins, V. C. Chambers, and R. S. Weiser. 1969. Antibody response in rainbow trout (*Salmo gairdneri*). I. Immunocompetent cells in the spleen and anterior kidney. J. Immunol. 102: 1193-1201.

Christensen, G. M., J. T. Fiandt, and B. A. Poeschl. 1978. Cells, proteins, and certain physical-chemical properties of brook trout (*Salvelinus fontinalis*) blood. J. Fish Biol. 12: 51-60.

Clawson, C. C., J. Finstad, and R. A. Good. 1966. Evolution of the immune response. V. Electron microscopy of plasma cells and lymphoid tissue of the paddlefish. Lab. Invest. 15: 1830-1847.

Conroy, D. A. 1972. Studies on the haematology of the Atlantic salmon (*Salmo salar* L.). Pages 101-127 *in* L. E. Mawdesley-Thomas, ed. Diseases of fish. Symp. Zool. Soc. No. 30. Academic Press, London.

Davis, J. C. 1970. Estimation of circulation time in rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 27: 1860-1863.

Ellis, A. E. 1976. Leucocytes and related cells in the plaice *Pleuronectes platessa*. J. Fish Biol. 8: 143-156.

Ellis, A. E. 1977. The leucocytes of fish: A review. J. Fish Biol. 11: 453-491.

Ellis, A. E., A. L. S. Munro, and R. J. Roberts. 1976. Defence mechanisms in fish. 1. A study of the phagocytic system and the fate of intraperitoneally injected particulate material in the plaice (*Pleuronectes platessa* L.). J. Fish Biol. 8: 67-78.

Ellis, A. E., and M. de Sousa. 1974. Phylogeny of the lymphoid system. I. A study of the fate of circulating lymphocytes in plaice. Eur. J. Immunol. 4: 338-343.

Enomoto, Y. 1969*a*. On some notes about the fluctuations of the blood leucocytes numbers of the cultured fish. Bull. Tokai Reg. Fish. Res. Lab. 57: 137-177.

Enomoto, Y. 1969*b*. Some notes on the fluctuations of the immature leucocyte number in the blood of cultured fish. Bull. Tokai Reg. Fish. Res. Lab. 58: 191-201.

Etlinger, H. M. 1975. Function and structure of rainbow trout leukocytes. Ph.D. Thesis. University of Washington, Seattle.

Etlinger, H. M., H. O. Hodgins, and J. M. Chiller. 1976*a*. Characterization of lymphocytes in a primitive teleost, *Salmo gairdneri*. Pages 83-91 *in* R. K. Wright and E. L. Cooper, eds. Phylogeny of thymus and bone marrow – bursa cells. North-Holland Publishing Co., New York.

Etlinger, H. M., H. O. Hodgins, and J. M. Chiller. 1976*b*. Evolution of the lymphoid system. I. Evidence for lymphocyte heterogeneity in rainbow trout revealed by the organ distribution of mitogenic responses. J. Immunol. 116: 1547-1553.

Etlinger, H. M., H. O. Hodgins, and J. M. Chiller. 1976*c*. Rainbow trout leukocyte culture: a simplified method. In Vitro 12: 599-601.

Ezzat, A. A., M. B. Shabna, and A. M. Farghaly. 1974. Studies on the blood characteristics of *Tilapia zilli* (Gervais). I. Blood cells. J. Fish Biol. 6: 1-12.

Fange, R. 1968. The formation of eosinophilic granulocytes in the oesophageal lymphomyeloid tissue in the elasmobranchs. Acta Zool. (Stockh.) 48: 155-161.

Ferguson, H. W. 1976. The ultrastructure of plaice (*Pleuronectes platessa*) leucocytes. J. Fish Biol. 8: 139-142.

Finn, J. P. 1970. The protective mechanisms in diseases of fish. Commonw. Bur. Anim. Health Vet. Bull. 40: 873-886.

Finn, J. P., and N. O. Nielsen. 1971. The inflammatory response of rainbow trout. J. Fish Biol. 3: 463-478.

Flood, M. T., R. F. Nigrelli, and J. F. Gennars, Jr. 1975. Some aspects of the ultrastructure of the "Stabchendrusenzellen," a peculiar cell associated with the endothelium of the bulbus arteriosus and with other fish tissues. J. Fish Biol. 7: 129-138.

Garavini, C., and P. Martelli. 1981. Alkaline phosphatase and peroxidase in goldfish (*Carassius auratus*) leukocytes. Basic Appl. Histochem. 25: 133-140.

Gardener, G. R., and P. P. Yevich. 1969. Studies on the blood morphology of three estuarine cyprinodontiform fishes. J. Fish. Res. Board Can. 26: 433-447.

Haider, G. 1972. Hematological studies on rainbow trout *Salmo gairdneri* Richardson. IV. Erythrocyte count and hematocrit. Hydrobiologie 37: 457-472.

Hardig, J. 1978. Maturation of circulating red blood cells in young Baltic salmon (*Salmo salar* L.). Acta Physiol. Scand. 102: 290-300.

Hatai, K. 1972*a*. Studies on the fate of intravascularly injected bacteria in fish. I. Changes in the number of cells of *Aeromonas liquefaciens* in the blood, liver and kidney of the eel. Fish Pathol. 7: 26-33.

Hatai, K. 1972*b*. Studies on the fate of intravascularly injected bacteria in fish. II. Changes in the number and composition of leucocytes in the blood of the eel. Fish Pathol. 7: 34-43.

Hawkins, R., and L. E. Mawdesley-Thomas. 1972. Fish haematology – a bibliography. J. Fish Biol. 4: 193-232.

Heckman, J. R., F. W. Allendorf, and J. C. Wright. 1971. Trout leucocytes: Growth in oxygenated cultures. Science 173: 246-247.

Hines, R. S., and D. T. Spira. 1973. Ichthyophthiriasis in the mirror carp. II. Leukocyte response. J. Fish Biol. 5: 527-534.

Iuchi, I. 1973. The post hatching transition of erythrocytes from larval to adult type in rainbow trout *Salmo gairdneri irideus*. J. Exp. Zool. 184: 383-396.

Jakowska, S. 1956. Morphologie et nomenclature des cellules du sang des teleosteens. Revue Hemat. 11: 519-539.

Jordan, H. E., and C. C. Speidel. 1924. Studies on lymphocytes. II. The origin, function and fate of the lymphocytes in fishes. J. Morphol. 38: 529-549.

Kalashnikova, Z. M. 1976. On the classification of morphological elements in the blood of fish. J. Ichthyol. 16: 459-472.

Kindred, J. E. 1971. An attempt at a subjective and objective classification of the acidophilic granulocytes of some marine fishes. Biol. Bull. (Woods Hole) 140: 416-426.

Klontz, G. W. 1972. Haematological techniques and the immune response in rainbow trout. Pages 89-99 *in* L. E. Mawdesley-Thomas, ed. Diseases of fish. Symp. Zool. Soc. Lond. No. 30. Academic Press, London.

Klontz, G. W., W. T. Yasutake, and A. J. Ross. 1966. Bacterial disease of the Salmonidae in the Western United States: Pathogenesis of furunculosis in rainbow trout. Am. J. Vet. Res. 27: 1455-1460.

Lehmann, J., and F. J. Sturenberg. 1975*a*. Haematologisch-serologische Substratuntersuchungen an der Regenbogenforelle (*Salmo gairdneri* Richardson). I. Methodik zur Blutentnahme und Blutuntersuchung bei Fischen. Gewasser Abwasser 53/54: 114-132.

Lehmann, J., and F. J. Sturenberg. 1975*b*. Haematologisch-serologische Substratuntersuchungen an der Regenbogenforelle (*Salmo gairdneri* Richardson). II. Beschreibung und Darstellung der wichtigsten Zellen in der Blutbildungsstatte und im peripheren Blutgefassystem. Gewasser Abwasser 55/56: 5-123.

Lester, R. J. G., and B. A. Daniels. 1976. The eosinophilic cell of the white sucker, *Catostomus commersoni*. J. Fish. Res. Board Can. 33: 139-144.

Lester, R. J. G., and S. S. Desser. 1975. Ultrastructural observations on the granulocytic leucocytes of the teleost *Catostomus commersoni*. Can. J. Zool. 53: 1648–1657.

Lewis, D. H., G. W. Klontz, S. McConnell, and L. C. Grumbles. 1970. Infectious disease and host response of marine fish, a partially annotated bibliography. Texas A&M University, Sea Grant Publ. No. TAMU-SG-71-401. 104 pp.

Lied, E., J. Gjerde, and O. R. Braekkan. 1975. Simple and rapid technique for repeated blood sampling in rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 32: 699–701.

Lientz, J. C., and C. E. Smith. 1974. Some hematological parameters for hatchery-reared cutthroat trout. Prog. Fish-Cult. 36: 49–50.

Lucas, A. M., and C. Jamroz. 1961. Atlas of avian hematology. U.S. Dep. Agric., Agric. Monogr. 25. 271 pp.

MacMillan, J. R. 1980. Pathologic manifestations of viral erythrocytic necrosis in fish. Ph.D. Thesis. University of Washington, Seattle. 165 pp.

Mahajan, C. L., and J. S. Dheer. 1979. Cell types in the peripheral blood of an air-breathing fish *Channa punctatus*. J. Fish Biol. 14: 481–487.

Matsusato, T. 1972. Primitive erythropoiesis in early development of amago *Oncorhynchus rhodurus* J., and rainbow trout *Salmo gairdneri irideus* G. Bull. Nansei Reg. Fish. Res. Lab. 5: 25–34.

McCarthy, D. H., J. P. Stevenson, and M. S. Roberts. 1973. Some blood parameters for the rainbow trout (*Salmo gairdneri* Richardson). I. The Kamloops variety. J. Fish Biol. 5: 1–8.

McCarthy, D. H., J. P. Stevenson, and M. S. Roberts. 1975. Some blood parameters of the rainbow trout (*Salmo gairdneri* Richardson). II. The Shasta variety. J. Fish Biol. 7: 215–219.

McLeay, D. J. 1975. Variations in the pituitary-interrenal axis and the abundance of circulating blood-cell types in juvenile coho salmon, *Oncorhynchus kisutch* during stream residence. Can. J. Zool. 53: 1882–1892.

Morrow, W. J. W., and A. Pulsford. 1980. Identification of peripheral blood leucocytes of the dogfish (*Scyliorhinus canicula* L.) by electron microscopy. J. Fish Biol. 17: 461–475.

Mulcahy, M. F. 1970. Blood values in the pike *Esox lucius* L. J. Fish Biol. 2: 203–209.

Nanba, K., H. Nakagawa, S. Murachi, M. Kayama, and T. Nakamura. 1973. Blood properties of cultured yellow tail, *Seriola quinqueradiata* Temminck and Schlegel. I. Effect of disease caused by anchovy *Engraulis javonica* Houttuyn, as diet. J. Fac. Fish. Anim. Husb. Hiroshima Univ. 12: 89–99.

Pickford, G. E., A. K. Srivastava, A. M. Slicher, and P. K. T. Pang. 1971*a*. The stress response in the abundance of circulating leucocytes in the killifish *Fundulus heteroclitus*. I. The cold shock sequence and the effects of hypophysectomy. J. Exp. Zool. 177: 89–96.

Pickford, G. E., A. K. Srivastava, A. M. Slicher, and P. K. T. Pang. 1971*b*. The stress response in the abundance of circulating leucocytes in the killifish *Fundulus heteroclitus*. II. The role of catecholamines. J. Exp. Zool. 177: 97–108.

Pickford, G. E., A. K. Srivastava, A. M. Slicher, and P. K. T. Pang. 1971*c*. The stress response in the abundance of circulating leucocytes in the killifish *Fundulus heteroclitus*. III. The role of the adrenal cortex and a concluding discussion of the leucocyte-stress syndrome. J. Exp. Zool. 177: 109–117.

Post, G. 1963. The immune response of rainbow trout to *Aeromonas hydrophila*. Utah Dep. Fish Game. Publ. 63-67. 82 pp.

Priede, I. G. 1973. The physiology of circulation during swimming activity in rainbow trout. Ph.D. Thesis. University of Stirling, Scotland.

Radzinskaya, L. I. 1968. Localization and amount of peroxidase in the embryonic development of the Neva salmon *Salmo salar*. Vopr. Ikhtiol. 8: 380–382.

Randall, D. J. 1968. Functional morphology of the heart in fishes. Am. Zool. 8: 179–189.

Rubashov, S. I. 1936. Investigations of the physiological blood of fish on the blood corpuscles of some freshwater fishes. Tr. Boroninsk. Biol. Stn. 9: 61–69.

Sakai, D. K. 1981. Separation of lymphocytes from the peripheral blood of rainbow trout and goldfish. Bull. Jpn. Soc. Sci. Fish. 47: 1281–1288.

Saito, K. 1959. Biochemical studies on the fish blood. XIV. On the mean corpuscular content and shape of red corpuscle. Mem. Fac. Fish. Kagoshima Univ. 7: 192–197.

Saunders, D. C. 1967. Neutrophils and arneth counts from some Red Sea fishes. Copeia 1967: 681–683.

Saunders, D. C. 1968. Variations in thrombocytes and small lymphocytes found in the circulating blood of marine fishes. Trans. Am. Microsc. Soc. 87: 39–43.

Sekhon, S. S., and H. W. Beams. 1969. Fine structure of the developing trout erythrocytes and thrombocytes with special reference to the marginal band and the cytoplasmic organelles. Am. J. Anat. 125: 353–374.

Sekhon, S. S., and D. S. Maxwell. 1970. Fine structure of developing hagfish erythrocytes with particular reference to the cytoplasmic organelles. J. Morphol. 131: 211–236.

Siddiqui, A. Q., and S. M. Naseem. 1979. The haematology of Rohu, *Labeo rohita*. J. Fish Biol. 14: 67–72.

Soivio, A., K. Nyholm, and K. Westman. 1973. Notes on haematocrit determinations on rainbow trout, *Salmo gairdneri*. Aquaculture 2: 31–35.

Soivio, A., K. Nyholm, and K. Westman. 1975. A technique for repeated sampling of the blood of individual resting fish. J. Exp. Biol. 62: 207–217.

Soivio, A., K. Westman, and K. Nyholm. 1974. Changes in haematocrit values in blood samples treated with and without oxygen: A comparative study with four salmonid species. J. Fish Biol. 6: 763–769.

Srivastava, A. K. 1968. Studies on the hematology of certain freshwater teleosts. I. Erythrocytes. Anat. Anz. 123: 233–249.

Srivastava, A. K. 1969. Studies on the hematology of certain freshwater teleosts. V. Thrombocytes and clotting of blood. Anat. Anz. 129: 368–374.

Stevens, E. D. 1968. The effect of exercise on the distribution of blood to various organs in rainbow trout. Comp. Biochem. Physiol. 25: 615–625.

Topf, W. 1955. Die Blutbildung und die Blutbildungsstatten beim Karpfen (*Cyprinus carpio* L.). Z. Fisch. Hilfswiss. 4: 257–288.

Van Vuren, J. H. J., and J. Hattingh. 1978. A seasonal study of the haematology of wild freshwater fish. J. Fish Biol. 13: 305–313.

Ward, J. W. 1969. Hematological studies on the Australian lungfish *Neoceratodus forsteri*. Copeia 1969: 633–635.

Wardle, C. S. 1971. New observations on the lymph system of the plaice, *Pleuronectes platessa* and other teleosts. J. Mar. Biol. Assoc. U. K. 51: 977–990.

Watson, M. E., R. W. Guenther, and R. D. Royce. 1956. Hematology of healthy and virus-diseased sockeye salmon, *Oncorhynchus nerka*. Zoologica 41: 27–37.

Wedemeyer, G., F. P. Meyer, and L. S. Smith. 1976. Environmental stress and fish diseases. Book 5 (192 pp.) *in* S. F. Snieszko and H. R. Axelrod, eds. Diseases of fishes. T. F. H. Publications, Inc., Neptune City, New Jersey.

Wedemeyer, G., and W. T. Yasutake. 1977. Clinical methods for the assessment of the effects of environmental stress on fish health. U.S. Fish Wildl. Serv., Tech. Pap. 89. 18 pp.

Weinberg, S. R., C. D. Siegel, and A. S. Gordon. 1973. Studies on the peripheral blood cell parameters and morphology of the red paradise fish, *Macropodus opercularis*. Effect of food deprivation on erythropoiesis. Anat. Rec. 175: 7–14.

Weinberg, S. R., C. D. Siegel, R. F. Nigrelli, and A. S. Gordon. 1972. The hematological parameters and blood cell morphology of the brown bullhead catfish, *Ictalurus nebulosus* (Le Sueur). Zoologica 57: 71–78.

Weinreb, E. L. 1963*a*. Electron microscope studies on teleost blood cells under normal and experimental conditions. Anat. Rec. 145: 369. (Abstr.)

Weinreb, E. L. 1963*b*. Studies on the fine structure of teleost blood cells. I. Peripheral blood. Anat. Rec. 147: 219–238.

Weinreb, E. L., and S. Weinreb. 1969. A study of experimentally induced endocytosis in a teleost. I. Light microscopy of peripheral blood cell responses. Zoologica 54: 25–37.

Whitmore, C. M. 1965. A microcytic anemia of juvenile chinook salmon resulting from diets deficient in vitamin E. Contrib. Fish Comm. Ore. 29: 1–31.

Williams, R. W., and M. C. Warner. 1976. Some observations on the stained blood cellular elements of channel catfish, *Ictalurus punctatus*. J. Fish Biol. 9: 491–497.

Yamamoto, M., and I. Iuchi. 1975. Electron microscopic study of erythrocytes in developing rainbow trout, *Salmo gairdnerii irideus*, with particular reference to changes in the cell line. J. Exp. Zool. 191: 407–426.

Yasutake, W. T. 1975. Fish virus diseases: Clinical, histopathological and comparative aspects. Pages 247–271 *in* A. E. Ribelin and G. Migaki, eds. The pathology of fishes. University of Wisconsin Press, Madison.

Yasutake, W. T. 1979. Histopathology of yearling sockeye salmon (*Oncorhynchus nerka*) infected with infectious hematopoietic necrosis (IHN). Fish Pathol. 14: 59–64.

Yasutake, W. T., and D. F. Amend. 1972. Some aspects of pathogenesis of infectious hematopoietic necrosis (IHN). J. Fish Biol. 4: 261–264.

Yokoyama, H. O. 1960. Studies on the origin, development and seasonal variations in the blood cells of the perch, *Perca flavescens*. Wildl. Dis. 6: 1–102.

Yuki, R. 1957. Blood cell constituents in fish. I. Peroxidase staining of the leucocytes in rainbow trout (*Salmo irideus*). Bull. Fac. Fish. Hokkaido Univ. 8: 36–44.

Yuki, R. 1958. Blood cell constituents in fish. II. Peroxidase staining of the leucocytes in the kidney and some other organs. Bull. Fac. Fish. Hokkaido Univ. 8: 264–269.

Yuki, R. 1960. Blood cell constituents in fish. IV. On the "nuclear shadow" found in blood smear preparation. Bull. Jpn. Soc. Sci. Fish. 26: 490–495.

Zapata, A. 1980. Ultrastructural study of erythropoiesis of teleost fish. Morfol. Norm. Patol. A-Histol. (Buchar.) 4: 159–165.

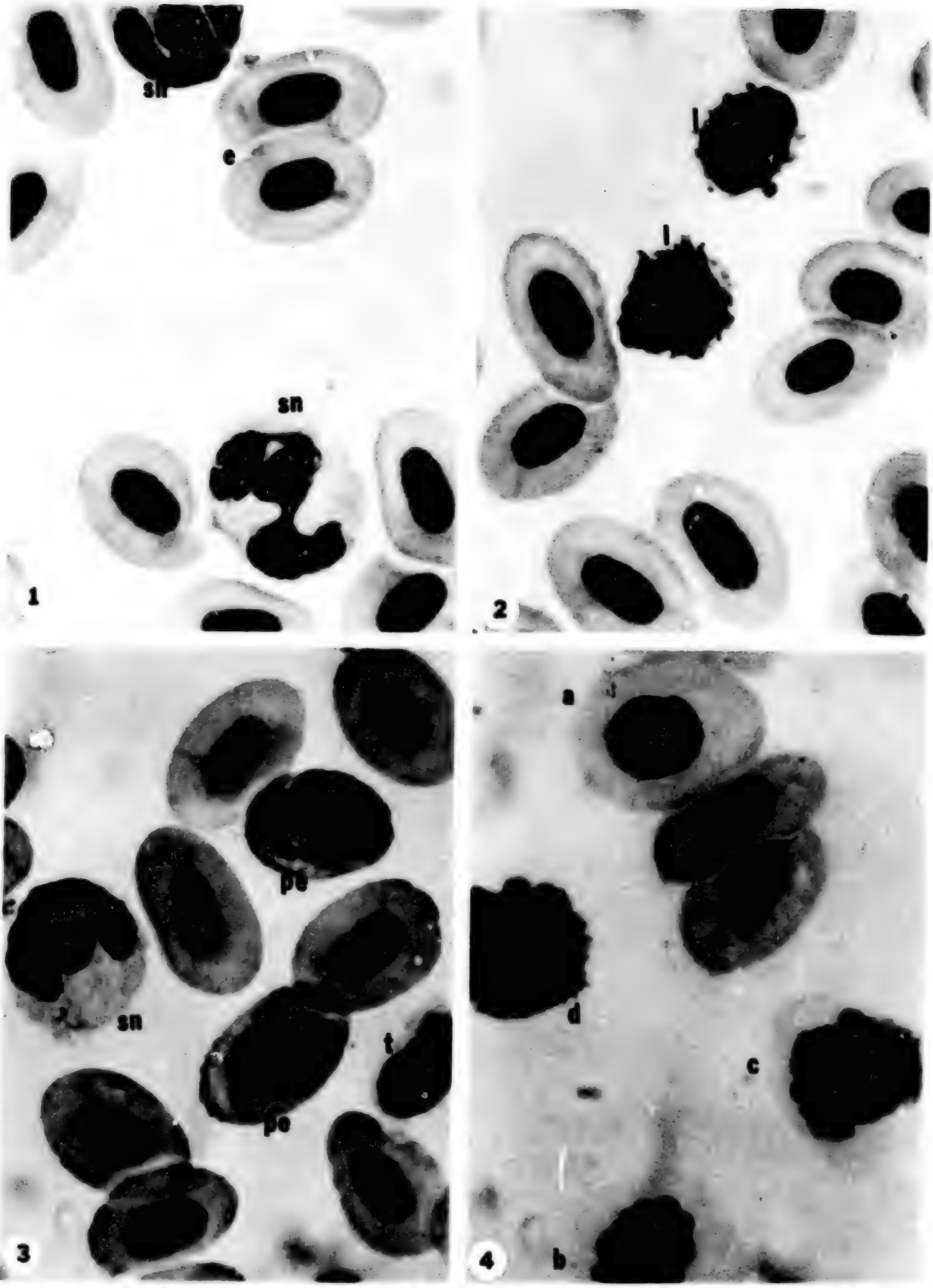


Plate 31. Blood (1). Peripheral blood smears from 4-month-old rainbow trout, stained with Leishman-Giemsa stain.

Fig. 1. Segmented neutrophil (sn) surrounded by mature erythrocytes (e). × 3600.

Fig. 2. Two mature lymphocytes (l) with pseudopodia, surrounded by erythrocytes. × 3400.

Fig. 3. Segmented neutrophils (sn), polychromatocyte or immature erythrocyte (pe), and thrombocyte (t). × 3600.

Fig. 4. Successive stages (a–d) of erythrocyte "degeneration," ending as a smudge cell (d). Some cytoplasm is still visible in b and c. × 3600.

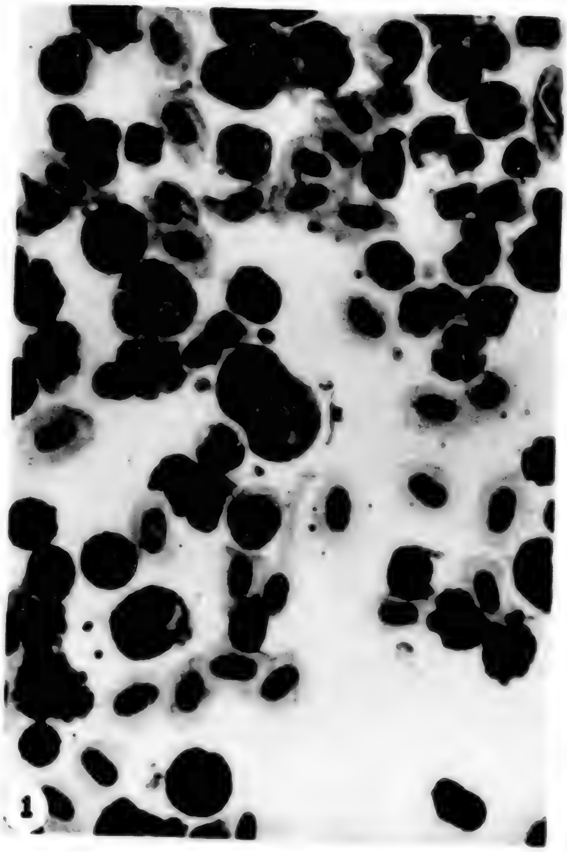
Plate 32. Blood (2). Imprints made from head kidneys of 4-month-old rainbow trout.

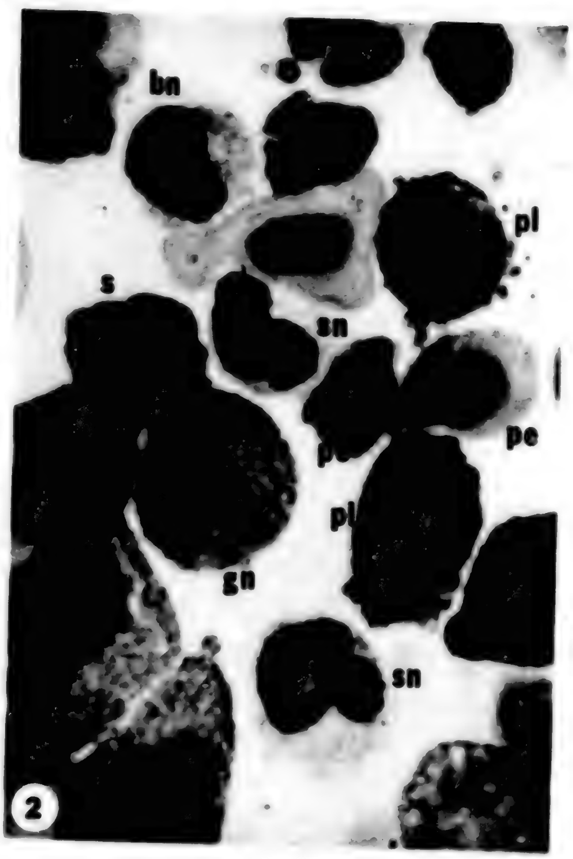
Fig. 1. Various states of hematopoiesis. Leishman-Giemsa stain. × 1700.

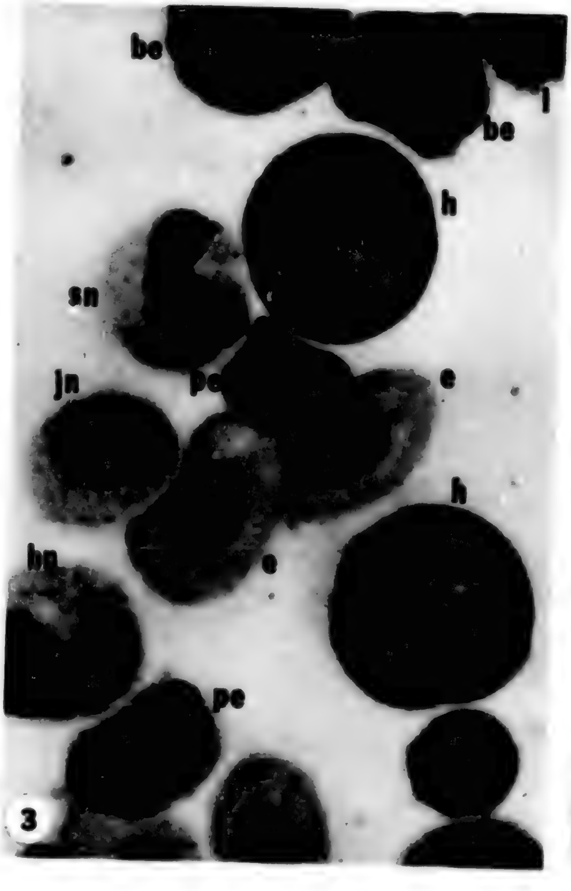
Fig. 2. Polychromatocyte (pe), an immature erythrocyte with basophilic cytoplasm; prolymphocyte (pl), an immature lymphocyte; granulocyte (gn), a very early immature neutrophil; segmented neutrophil (sn); band neutrophil (bn); mature neutrophil; smudge cell or degenerated erythrocyte (s). At the lower left is an immature cell that has undergone cell division. Leishman-Giemsa stain. × 3400.

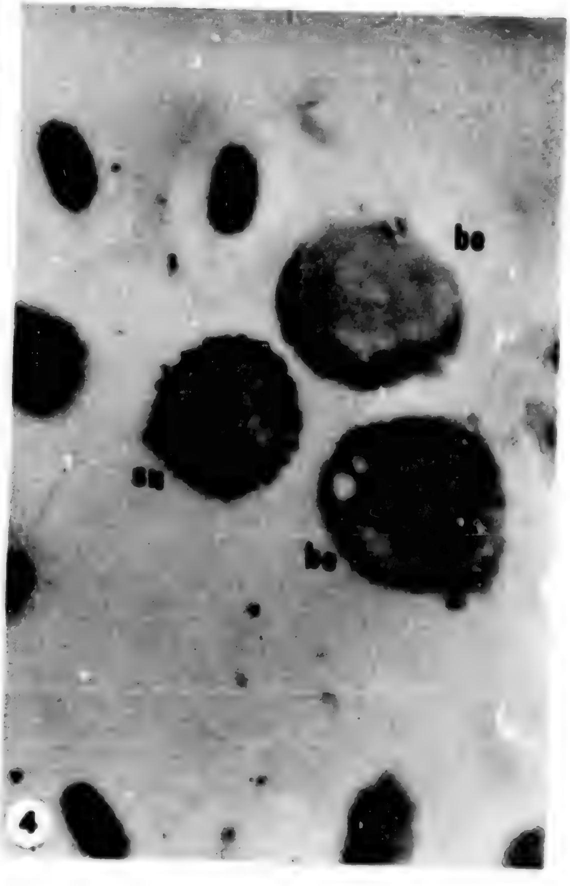
Fig. 3. Hemocytoblast (h) or stem cell; erythroblast (be), a very early stage of an erythrocyte; polychromatocyte (pe); mature erythrocyte (e); juvenile neutrophil (jn); band neutrophil (bn); segmented neutrophil (sn); mature lymphocyte (l). Leishman-Giemsa stain. × 3710.

Fig. 4. Segmented neutrophil (sn) with dark granules, reacting positively to the peroxidase stain. The larger cells (be) appear to be erythroblasts. Peroxidase stain. × 3700.


1


bn
pl
s
sn
pe
pl
pl
gn
sn
2


be
l
be
h
sn
jn
pe
e
h
e
bn
pe
3


be
sn
be
4

Blank Page

Chapter VIII

Hematopoietic Tissues

Hematopoietic Kidney

Bone marrow, spleen, and lymph nodes are the principal blood-forming tissues of warm-blooded vertebrates. In most fishes, including the rainbow trout, the primary site of hematopoiesis is in the anterior one-fourth of the kidney (Plate 35, Fig. 1). Posteriorly, much of the extrarenal tissue is also composed of blood-forming tissue. This tissue throughout the kidney is supported by a delicate reticular cell stroma and fibers (Leenhuer 1969). Tissue imprints of the head kidney (Plate 32) show the various types of blood cells that are usually found in this area. Since it is the primary tissue of hematopoiesis, many undifferentiated (stem or blast) cells, as well as immature and mature red blood cells and white blood cells, are present.

Also present in the hematopoietic tissue are melanophore, melanin-containing cells (see Chapter 3). They are usually diffusely located (Plate 36, Fig. 1; Plate 60) and do not occur as discrete melanin-macrophage centers, such as those found in many other teleosts (Roberts 1975, 1978). According to Roberts (1975) the degree of pigmentation varies, depending on the species, age, and state of health of the fish.

Spleen

The spleen in most fishes serves as an accessory hematopoietic organ; it also serves as the site for blood cell destruction and for erythrocyte storage. It differs primarily from mammalian spleen in two respects: (1) red and white pulps are diffuse and not very discrete, and (2) connective tissue framework is not prominent (Robertson and Wexler 1960; Plate 33, Figs. 1–4). When the red pulp area is filled with red blood cells, the white pulp nodules (mostly lymphatic tissue) may be seen more readily (Plate 33, Fig. 2). The spleen capsule of trout is a thin layer of connective tissue and is not as thick or prominent as the capsule of the mammalian spleen.

Thymus Gland

The bilateral thymus glands in rainbow trout are located under the operculum and dorsal to the gill arches, where the operculum joins the body. In fingerlings 1–4 months old, the glands may be difficult to see; however, in fish 5–12 months old, the small opaque tissues can usually be seen with little difficulty. Histologically, the rainbow trout thymus is not unlike that of *Tilapia mossambica* (Sailendri and Muthukkaruppan 1975) and most other fishes. It is encapsulated by thin collagen-like fibers (Plate 34, Fig. 3). The gland consists mostly of lymphoid cells, including thymocytes and lymphocytes (in various stages of maturation), and some erythrocytes and macrophages (Plate 34, Fig. 3). Depending on the area and plane of section, gland-like cells – thymic bodies – are occasionally seen in the thymus (Plate 34, Fig. 4). The function of these cells is not known, but it has been suggested that they are comparable to the Hassel's corpuscles found in the thymus of mammals (Sailendri and Muthukkaruppan 1975).

References

Leenhuer, E. L. 1969. Hemopoiesis in the kidney of *Oncorhynchus masou* (Brevoort). M.S. Thesis. University of Western Ontario, London.

Mahajan, C. L., and J. M. S. Dheer. 1980. An autoradiographic and cytochemical study of erythropoiesis in a fresh water fish, *Channa punctatus* Bloch. J. Fish Biol. 17: 641–648.

McArdle, J. F., and R. J. Roberts. 1974. Bilateral hyperplasia of the thymus in a rainbow trout (*Salmo gairdneri*). J. Fish. Res. Board Can. 31: 1537–1539.

Norris, E. R., and R. W. Simmons. 1945. The hematopoietic activity of xanthopterin in young salmon. J. Biol. Chem. 24: 449–453.

Pestova, I. M. 1956. The hematopoietic faculty of the vascular endothelium in the otogenesis of bony fish. Arkh. Anat. Gistol. Embriol. 31: 17–24.

Remmele, W., and F. Rodrequez-Erdmann. 1959. The kidneys and erythropoiesis. Frankf. Z. Pathol. 70: 152–173.

Roberts, R. J. 1975. Melanin-containing cells of teleost fish and their relation to disease. Pages 399–428 *in* W. E. Ribelin and G. Migaki, eds. The pathology of fishes. University of Wisconsin Press, Madison.

Roberts, R. J. 1978. Fish pathology. Bailliere Tendall, London. 318 pp.

Robertson, O. H., and B. C. Wexler. 1960. Histological changes in the organs and tissues of migrating and spawning Pacific salmon (genus *Oncorhynchus*). Endocrinology 66: 222–239.

Sailendri, K., and V. R. Muthukkaruppan. 1975. Morphology of lymphoid organs in a cichlid teleost, *Tilapia mossambica*. J. Morphol. 147: 109–121.

Tamura, E. E., and Y. Honma. 1970. Histological changes in the organs and tissues of the gobiid fishes throughout the life-span. III. Hemapoietic organs in the ice-goby *Leucopsarion petersi* (Hilgendorf). Bull. Jpn. Soc. Sci. Fish. 36: 661–669.

Tatner, M. F., and M. J. Manning. 1982. The morphology of the trout, *Salmo gairdneri* Richardson, thymus: some practical and theoretical considerations. J. Fish Biol. 21: 27–32.

Zanjani, E. D., Y. Man-Lim, A. Perlmutter, and A. S. Gordon. 1969. Humoral factors influencing erythropoiesis in the fish blue gourami *Trichogaster trichopterus*. Blood 33: 537–581.

Zapata, A. 1980. Ultrastructural study of erythropoiesis of teleost fish. Morfol. Norm. Patol. Section A. 4: 159–178.

Plate 33. Spleen

Fig. 1. Longitudinal section through the abdominal viscera of a 1-month-old rainbow trout, showing position of the spleen in relation to adjacent tissues. × 40.

- a. Spleen
- b. Pancreas
- c. Visceral fat
- d. Villi of the anterior intestine
- e. Muscular wall of stomach
- f. Skin

Fig. 2. Detail of spleen (Fig. 1). × 250.

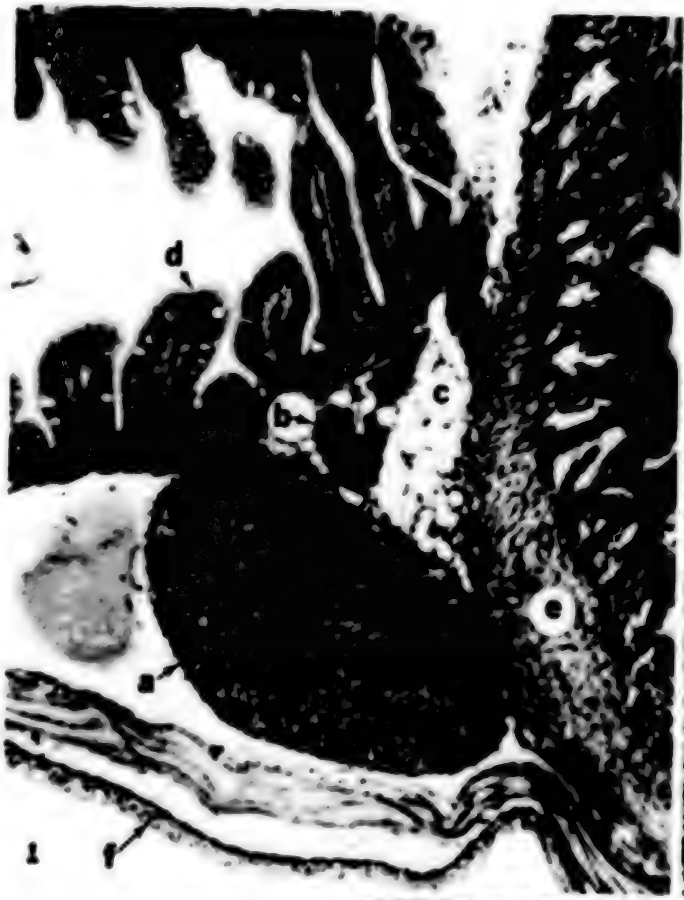
- a. Germinal node (white pulp)
- b. Stroma of reticular connective tissue with red blood cells (red pulp)

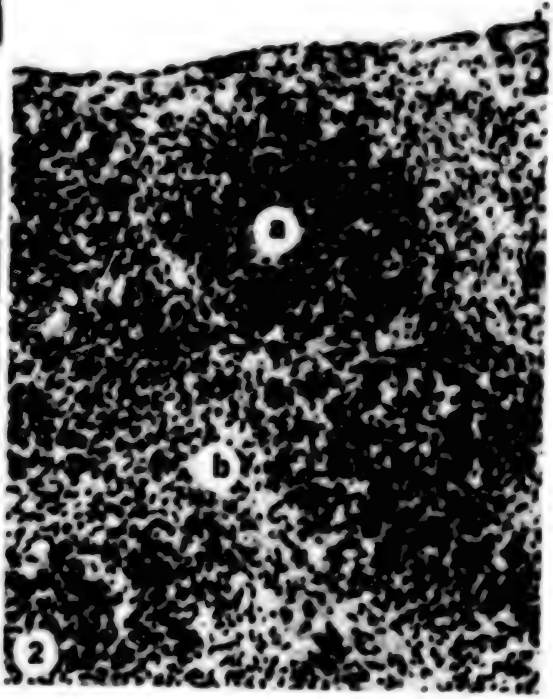
Fig. 3. Spleen of underyearling rainbow trout, showing arrangement of pulp and stroma. Each nodule of pulp forms a surface protrusion. × 35.

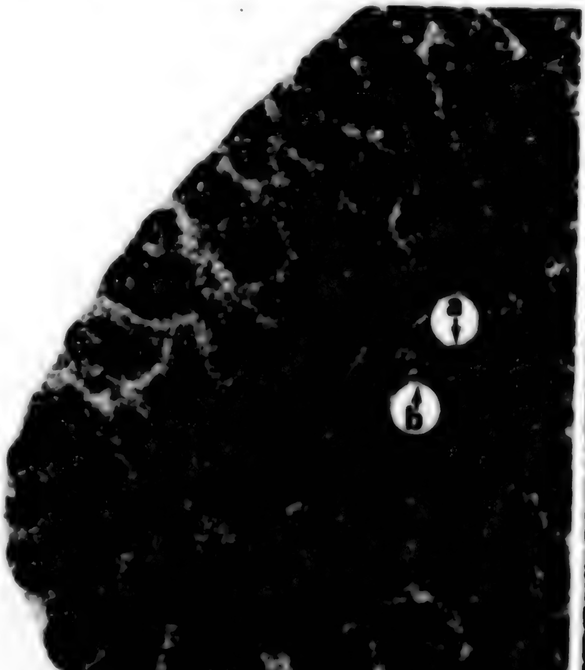
- a. Vein filled with erythrocytes
- b. Arteriole

Fig. 4. Detail of Fig. 3. × 250.

- a. Capsule of spleen
- b. Connective tissue stroma
- c. Surface protrusion filled with erythrocytes


d
b
c
e
a
f
1


a
b
2


a
b
3

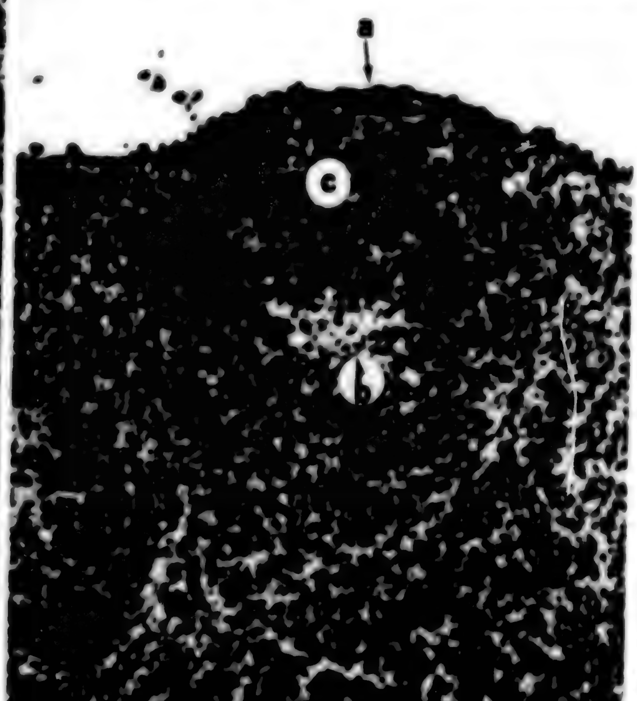

a
c
b
4

Plate 34. Thymus

Fig. 1. Longitudinal section through head of 1-month-old rainbow trout. × 50.

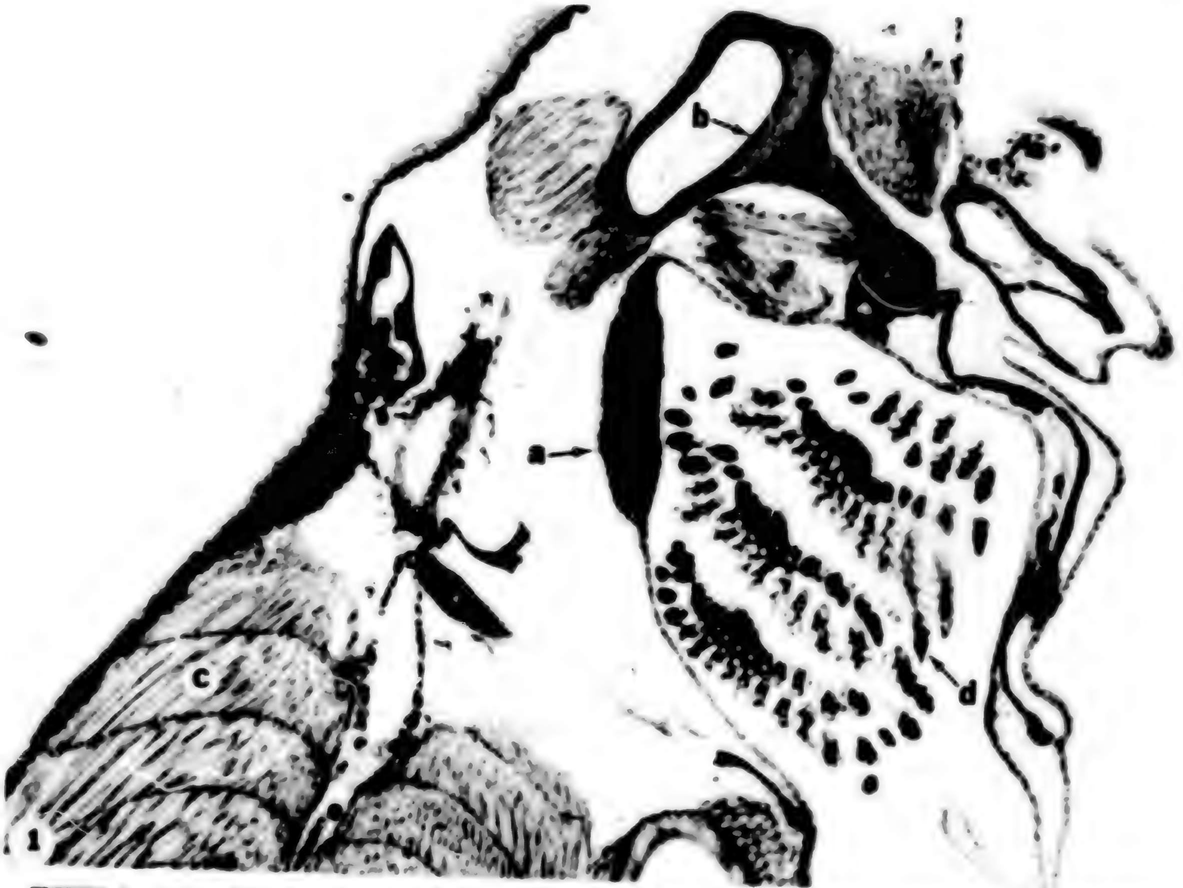
a. Thymus gland
b. Cartilage of the otic capsule
c. Dorsal musculature
d. Gills

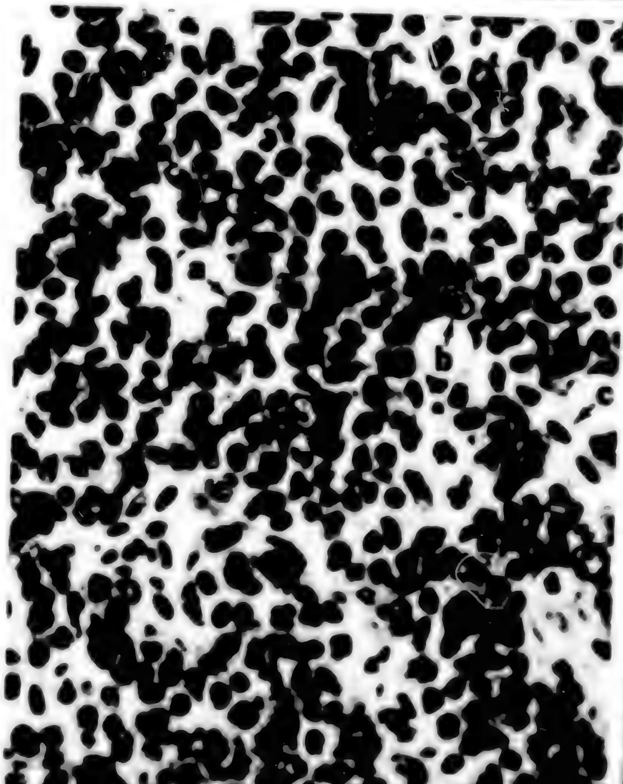
Fig. 2. Detail of Fig. 1. × 560.

a. Thymocyte
b. Reticular cell
c. Erythrocyte

Fig. 3. Edge of thymus gland of 3-month-old rainbow trout. × 200.

a. Thymic body, presumed to be comparable to Hassel's corpuscle in mammals
b. Capsule
c. Thymocytes


b
a
c
d
1


b
c
2

b
c
3

Blank Page

Chapter IX

Urinary System

by

J. D. Hendricks

Oregon State University
Corvallis, Oregon

Fish kidneys are the least readily recognized fish organs, due to their lack of similarity to mammalian kidneys. The kidneys of fishes generally occupy a dorsal position along most of the length of the body cavity. In trout they compose the dorsal blood-filled structure that remains after the other viscera are removed. Although their structure appears single, they are composed of two almost completely fused kidneys, each with its own mesonephric duct. These ducts become visible posteriorly, as they leave the kidneys and unite to form the common urinary duct and bladder leading to the urogenital papillae. Anteriorly the kidneys are composed entirely of hematopoietic tissue known as the head kidney (Plate 35, Fig. 1) and more posteriorly of nephrons embedded in hematopoietic tissue. In addition to urinary and blood-forming tissues, the kidney also includes adrenal tissues and the Corpuscles of Stannius. Juxtaglomerular cells, considered to be homologous to those of mammals (Harder 1975), have also been described in kidneys of trout (Oguri 1980*a*) and other teleosts (Oguri and Sokabe 1968; Capreol and Sutherland 1968; Oguri et al. 1969; Oguri 1980*b*). These cells produce renin, a proteolytic enzyme necessary for the production of angiotensin II, which in turn influences blood pressure and urine formation (Capreol and Sutherland 1968; Harder 1975). Oguri (1980*a*) stated that the juxtaglomerular cells stain well with Bowie's method and are periodic acid-Schiff positive.

The principal function of teleost kidneys is the maintenance of a stable internal environment with respect to water and salts, and not the excretion of metabolic nitrogenous wastes, as in tetrapods. Although small amounts of nitrogenous wastes – i.e., ammonia, urea, creatine, creatinine, and trimethylamine oxide – do appear in the urine, this excretory route is incidental when compared with the amounts of these products that are excreted through the primary excretory organs, the gills (Smith 1929).

Teleosts have three major nephron types with regard to structure and function: the freshwater glomerular nephron, the marine glomerular nephron, and the marine aglomerular nephron. Rainbow trout have a typical freshwater glomerular nephron that consists of the following regions: a renal corpuscle, made up of Bowman's capsule and the glomerulus; a short neck segment; two morphologically distinct segments of the proximal tubule (each with a brush border); a variably present intermediate segment; a distal segment; and a collecting duct system terminating in the mesonephric duct (Grafflin 1937*a*). Major functions of the freshwater teleost nephron are conservation of salt and elimination of excess water. These functions are accomplished by a high glomerular filtration rate, reabsorption of salts in the proximal tubules, and further urine dilution in the distal segment.

Histologically the nephron is similar throughout the salmonid group. There is disagreement on the best way to classify the terminal part of the second proximal segment in rainbow trout. Hickman and Trump (1969) reported that the terminal portion of the second proximal segment is ciliated, and designated that region as an intermediate segment. Anderson and Loewen (1975) also described a very short, distinctive segment. Ultrastructurally the cells were cuboidal and had varying numbers of apical cilia and no brush border. The cilia are sometimes distinguishable in this portion of the rainbow trout nephron, but the electron microscope is needed to distinguish these cells from those of the second proximal segment. The cells of this region stain the same as those of the second proximal segment, and numerous sections show the abrupt change from the strongly eosinophilic proximal tubule cells to the weakly eosinophilic distal tubule cells (Plate 36, Figs. 2 and 3).

The glomeruli of rainbow trout kidneys are large and nearly fill Bowman's capsule, which is the expanded funnel-like proximal end of the nephron. The larger afferent and smaller efferent glomerular arterioles, which supply and drain the glomerular capillary bed, can often be seen at the pole of the renal corpuscle. Within the structure of the glomerulus, nucleated red blood cells can be distinguished in the capillary lumens, as can the nuclei of mesangial cells, capillary endothelial cells, and the podocytes of the visceral epithelium of Bowman's capsule. After periodic acid-Schiff staining, the basement membrane, which lies between the mesangian and capillary endothelial cell layers, can also be seen. The parietal layer of Bowman's capsule consists of thin squamous cells, which become cuboidal toward the opening of the neck segment (Plate 35, Fig. 2).

The neck segment varies in length but is always short, and sometimes almost undetectable. Cross sections of this region are rarely seen in prepared slides. The cells are low columnar and narrow, with elongated, basally located nuclei and slightly basophilic cytoplasm. Cilia project into the tubular lumen but there is no brush border in this region. The narrow lumen of this segment, together with the low columnar cells, results in the overall diameter of the tubule being small (Plate 35, Fig. 2).

The transition to the first segment of the proximal tubule is abrupt (Plate 35, Fig. 2). The cells of this region are taller columnar, having rounded or oval, basally located nuclei, a prominent apical brush border, and lightly eosinophilic cytoplasm. The cytoplasm often appears bizonal, with an intensely staining basal region and a more lightly staining apical region. The larger lumen and taller cells make the overall tubular diameter much greater than that of the neck segment (Plate 35, Figs. 2-4; Plate 36, Figs. 1 and 3).

Another abrupt transition occurs between the first and second segments of the proximal tubule (Plate 35, Fig. 4). The second segment is characterized by even taller columnar cells that have rounded to oval, centrally located nuclei; a dense apical brush border; and intensely eosinophilic cytoplasm. The lumen is smaller than in the first segment of the proximal tubule and often appears occluded by the brush border. The overall tubular diameter is greater, however, because the cells are taller (Plate 35, Figs. 3 and 4; Plate 36, Figs. 1-3).

The change from the intensely staining second proximal segment to the lightly eosinophilic distal tubule is again abrupt (Plate 36, Fig. 2). The cells are lower columnar with oval, basally located nuclei and no brush border. The lumen is small, resulting in a smaller overall diameter (Plate 36, Figs. 1-3).

It is difficult to determine exactly where the distal tubule ends and the collecting duct begins because the staining characteristics of the two regions are similar. Hendricks (1971) designated the collecting duct as the portion of the tubule beyond the first junction with another tubule. Electron microscopy may show cytological differences before this junction, but light microscopy does not. Beyond the first junction, the collecting duct increases in size as it receives additional nephrons. The cells increase in height (but remain lightly eosinophilic), the lumen size increases, and the amount of surrounding smooth muscle and connective tissue increases as the collecting duct approaches the mesonephric duct (Plate 36, Figs. 3 and 4). The large mesonephric duct has tall columnar, lightly staining cells, with elongated, basally located nuclei and large amounts of surrounding smooth muscle and connective tissue (Plate 36, Fig. 4).

Another distinct tubule is present in fish kidneys, especially in immature fish. The cells are characterized by deeply basophilic cytoplasm, large irregular nuclei, and frequent mitotic figures. These tubules are immature, developing nephrons that become functional at a later date. They appear to develop in place from nephrogenic material and develop a connection with a collecting duct before becoming functional. Immature tubules of varying degrees of basophilia are present in the kidneys of young trout (Plate 36, Fig. 5).

Some nuclei adhere closely to the exterior of each of the tubular regions. Electron microscopy has shown these to belong to smooth muscle cells that surround the tubules (Bulger and Trump 1968). The cytoplasm of these cells is difficult to see, being thinly spread over the surface of the tubule.

Darkly stained cells that are frequently between the epithelial cells of the tubules are wandering lymphoid cells from the adjacent hematopoietic tissue, which migrate to the tubular lumens in substantial numbers.

References

Anderson, B. G., and R. D. Loewen. 1975. Renal morphology of freshwater trout. Am. J. Anat. 143: 93–113.

Beitch, I. 1963. A histomorphological comparison of the urinary system in the serranid fishes, *Roccus saxatilis* and *R. americanus*. Chesapeake Sci. 4: 75–83.

Bulger, R. E., and B. F. Trump. 1965. A light and electron microscopic study of the mesonephric kidney of the English sole, *Parophrys vetulus*. Anat. Rec. 151: 445. (Abstr.)

Bulger, R. E., and B. F. Trump. 1968. Renal morphology of the English sole (*Parophrys vetulus*). Am. J. Anat. 123: 195–226.

Bulger, R. E., and B. F. Trump. 1969*a*. Ultrastructure of granulated arteriolar cells (juxtaglomerular cells) in kidney of a fresh and a salt water teleost. Am. J. Anat. 124: 77–87.

Bulger, R. E., and B. F. Trump. 1969*b*. Ca^{++} and K^{+} ion effects on ultrastructure of isolated flounder kidney tubules. J. Ultrastruct. Res. 28: 301–319.

Capreol, S. V., and L. E. Sutherland. 1968. Comparative morphology of juxtaglomerular cells. I. Juxtaglomerular cells in fish. Can. J. Zool. 46: 249–256.

de Ruiter, A. J. H. 1980. Changes in glomerular structure after sexual maturation and seawater adaptation in males of the euryhaline teleost *Gasterosteus aculeatus* L. Cell Tissue Res. 206: 1–20.

Desmet, W. 1963. The nephron of *Amia calva* (Protospondyli, Pisces). Acta Zool. (Stockh.) 44: 269–298.

Dobbs, G. H., III, Y. Lin, and A. L. DeVries. 1974. Aglomerularism in Antarctic fish. Science 185: 793–794.

Edwards, J. G. 1928*a*. Studies on aglomerular and glomerular kidneys. II. Physiology. Am. J. Physiol. 86: 383–398.

Edwards, J. G. 1928*b*. Studies on aglomerular and glomerular kidneys. I. Anatomical. Am. J. Anat. 42: 75–107.

Edwards, J. G. 1929. Studies on aglomerular and glomerular kidneys. III. Cytological. Anat. Rec. 44: 15–27.

Edwards, J. G. 1935. The epithelium of the renal tubule in bony fish. Anat. Rec. 63: 263–279.

Edwards, J. G., and C. Schnetter. 1933. The renal unit in the kidney of vertebrates. Am. J. Anat. 53: 55–87.

Endo, M., and M. Kimura. 1982. Histological and enzyme histochemical studies on the nephrons of the freshwater fishes, *Cyprinus carpio* and *Carassius auratus*. J. Morphol. 173: 29–34.

Ericsson, J. L. E., and S. Olsen. 1970. On the fine structure of the aglomerular renal tubule in *Lophius piscatorius*. Z. Zellforsch. Mikrosk. Anat. 104: 240–258.

Ford, P. 1958. Studies on the development of the kidney of the Pacific pink salmon, *Oncorhynchus gorbuscha* (Walbaum). II. Variation in glomerular count in the kidney of the Pacific pink salmon. Can. J. Zool. 37: 45–47.

Ford, P., and J. D. Newstead. 1958. Studies on the development of the kidney of the Pacific pink salmon *Oncorhynchus gorbuscha* (Walbaum). I. The development of the pronephros. Can. J. Zool. 36: 15–21.

Forster, R. P. 1953. A comparative study of renal function in marine teleosts. J. Cell. Comp. Physiol. 42: 487–510.

Grafflin, A. L. 1931. The structure of the renal tubule of the toadfish. Bull. Johns Hopkins Hosp. 48: 269–271.

Grafflin, A. L. 1933. Glomerular degeneration in the kidney of the daddy sculpin (*Myoxocephalus scorpius*). Anat. Rec. 57: 59–79.

Grafflin, A. L. 1937*a*. Observations upon the structure of the nephron in the common eel. Am. J. Anat. 61: 21–62.

Grafflin, A. L. 1937*b*. The structure of the nephron in fishes. Anat. Rec. 68: 287–303.

Grafflin, A. L. 1937*c*. The problem of adaptation to fresh and salt water in the teleosts, viewed from the standpoint of the structure of the renal tubule. J. Cell. Comp. Physiol. 9: 469–476.

Gritzka, T. L. 1963. The ultrastructure of the proximal convoluted tubule of a euryhaline teleost, *Fundulus heteroclitus*. Anat. Rec. 145: 235–236.

Harder, W. 1975. Anatomy of fishes. E. Schweizerbart'sche Verlagsbuchhandlung (Nagel. u. Obermiller) Stuttgart. Part I: 612 pp. (Transl. from German)

Heath-Eves, M. J., and D. B. McMillan. 1974. The morphology of the kidney of the Atlantic hagfish, *Myxine glutinosa* (L.). Am. J. Anat. 139: 309–334.

Henderson, N. E. 1967. The urinary and genital systems of trout. J. Fish. Res. Board Can. 24: 447–449.

Hendricks, J. D. 1971. Histological and histochemical changes occurring in the kidneys of coho salmon smolts (*Oncorhynchus kisutch*) upon transfer to hypertonic and hypotonic salt solutions. Ph.D. Thesis. Colorado State University, Ft. Collins. 185 pp.

Hentschel, H., and H. Finkenstadt. 1980. Perfusion fixation and alcian-blue PAS staining in histology and histopathology of teleost kidney. J. Fish Dis. 3: 473–479.

Hickman, C. P., Jr. 1965. Studies on renal function in freshwater teleost fish. Trans. R. Soc. Can. (Ser. 4) 3: 213–236.

Hickman, C. P., Jr. 1968. Ingestion, intestinal absorption and elimination of seawater and salts in the southern flounder, *Paralichthys lethostigma*. Can. J. Zool. 46: 457–466.

Hickman, C. P., Jr., and B. F. Trump. 1969. The kidney. Pages 91–240 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 1. Academic Press, New York.

Holmes, W. N., and I. M. Stainer. 1966. Studies on the renal excretion of electrolytes by the trout *Salmo gairdneri*. J. Exp. Biol. 44: 33–46.

Kendall, M. W. 1978. Renal tubular morphology in rainbow trout. Anat. Rec. 190: 441.

Kendall, M. W., and D. E. Hinton. 1974. Renal tubular morphology in the channel catfish (*Ictalurus punctatus*) kidney. J. Fish Res. Board Can. 31: 346–347.

Komuro, T., and T. Yamamoto. 1975. The renal chloride cell of the freshwater catfish, *Parasilurus asotus*, with special reference to the tubular membrane system. Cell Tissue Res. 160: 263–271.

Koul, B. F. 1974. A note on the presence of "giant glomeruli" in a sisorid catfish *Glyptothorax kashmirensis* Hora. Current Sci. (Bangalore) 43: 256.

Lagios, M. D. 1974. Granular epithelioid (juxtaglomerular) cell and renovascular morphology of the coelacanth *Latimeria chalumnae* Smith (Crossopterygii) compared with that of other fishes. Gen. Comp. Endocrinol. 22: 296–307.

Lahlou, B., I. W. Henderson, and W. H. Sawyer. 1979. Renal adaptations by *Opsanus tau*, a euryhaline aglomerular teleost, to dilute media. Am. J. Physiol. 216: 1266–1272.

Leenheer, E. L. 1969. Hemopoiesis in the kidney of *Oncorhynchus masou* (Brevoort). M.S. Thesis. University of Western Ontario, London.

Liu, H. C. 1962. The comparative structure of the ureter. Am. J. Anat. 111: 1–16.

Marshall, E. K., Jr. 1929. The aglomerular kidney of the toadfish *Opsanus tau*. Bull. Johns Hopkins Hosp. 45: 95–100.

Marshall, E. K., Jr., and A. L. Grafflin. 1928. The structure and function of the kidney of *Lophius piscatorius*. Bull. Johns Hopkins Hosp. 43: 205–230.

Maunsbach, A. B. 1964. Comparison of renal tubule ultrastructure after perfusion fixation with different fixatives. J. Cell Biol 23: 108A–109A.

Nash, J. 1931. The number and size of glomeruli in the kidneys of fishes, with observations on the morphology of the renal tubules of fishes. Am. J. Anat. 47: 425–445.

Newstead, J. D., and P. Ford. 1960. Studies on the development of the kidney of the Pacific pink salmon (*Oncorhynchus gorbuscha* Walbaum). III. The development of the mesonephrons with particular reference to the mesonephric tubules. Can. J. Zool. 38: 1–7.

Ogawa, M. 1961. Histological changes of the kidney of goldfish in sea water. Sci. Rep. Saitama Univ. Series B., Vol. B: 1–20.

Oguri, M. 1976. Histochemical observations on the dark brown pigment granules found in the kidney tissue of rainbow trout. Bull. Jpn. Soc. Sci. Fish. 42: 1223–1227.

Oguri, M. 1980*a*. Presence of juxtaglomerular cells in trout kidneys. Bull. Jpn. Soc. Sci. Fish. 46: 295–297.

Oguri, M. 1980*b*. A histological investigation of the juxtaglomerular cell granules in fish kidneys. Bull. Jpn. Soc. Sci. Fish. 46: 797–800.

Oguri, M., and H. Sokabe. 1968. Juxtaglomerular cells in the teleost kidneys. Bull. Jpn. Soc. Sci. Fish. 34: 882–888.

Oguri, M., K. Kamiya, and H. Sokabe. 1969. A histological study of the juxtaglomerular cells in the kidney of Japanese mackerel. Bull. Jpn. Soc. Sci. Fish. 35: 737–742.

Oguri, M., M. Ogawa, and H. Sokabe. 1970. Absence of juxtaglomerular cells in the kidneys of Chondrichthyes and Cyclostomi. Bull. Jpn. Soc. Sci. Fish. 36: 881–884.

Olivereau, M., and J. Olivereau. 1977. Effect of transfer to salt water and back to fresh water on the histological structure of the eel kidney. J. Comp. Physiol. 115: 223–239.

Olsen, T. S. 1966. Ultrastructure of the base of renal tubule cells of marine teleosts. Nature (Lond.) 212: 95–96.

Pak Poy, R. K. F. 1958. Electron microscopy of the piscine *Carassius auratus* renal glomerulus. Anat. J. Exp. Biol. 36: 191–210.

Rasquin, P. 1969. Undescribed glands in the kidney of the juvenile tarpon, *Megalops atlantica*. Copeia 1969: 83–91.

Smith, H. W. 1929. The excretion of ammonia and urea by the gills of fish. J. Biol. Chem. 81: 727–742.

Tampi, P. R. S. 1959. On the renal unit in some common teleosts. Proc. Indian Acad. Sci. (B) 50: 88–104.

von Bielek, E. 1974. The development of the kidney of the grayling *Thymallus thymallus* L. and the pike *Esox lucius* L. Zool. Anat. Board 92: 163–180.

Watanabe, T. 1982. The cells with intracytoplasmic calcium-rich granules in the kidneys of salmonid fishes. Bull. Jpn. Soc. Sci. Fish. 48: 15–20.

Weatherley, A. H. 1963. A note on the head kidney and kidney of the perch *Perca fluviatilis* (Linnaeus), with special reference to the blood vascular system. J. Zool. (Lond.) 140: 161–167.

Wendelaar Bonga, S. E. 1973. Morphometrical analysis with the light and electron microscope of the kidney of the anadromous three-spined stickleback *Gasterosteus aculeatus*, form *trachurus*, from fresh water and from sea water. Z. Zellforsch. Mikrosk. Anat. 137: 563–588.

Youson, J. H. 1970. Observations on the opisthonephric kidney of the sea lamprey of the Great Lakes, *Petromyzon marinus* L. at various stages during the life cycle. Can. J. Zool. 48: 1313–1316.

Youson, J. H. 1971*a*. Interbular circulation in the opisthonephric kidney of the adult and larval sea lamprey, *Petromyzon marinus* L. Anat. Rec. 170: 401–412.

Youson, J. H. 1971*b*. Prismatic cristae and matrix granules in mitochondria of the kidneys of ammocoetes. J. Cell Biol. 48: 189–191.

Youson, J. H., and D. B. McMillan. 1970. The opisthonephric kidney of the sea lamprey of the Great Lakes, *Petromyzon marinus* (L.). II. Neck and proximal segments of the tubular nephron. Am. J. Anat. 127: 233–258.

Plate 35. Kidney (1)

Fig. 1. Rainbow trout kidney, showing transition from the hematopoietic tissue of the head kidney to the tubules (arrows) embedded in hematopoietic tissue of the posterior kidney. ×40.

Fig. 2. Proximal end of a nephron, showing a tubule leaving a renal corpuscle. ×700.

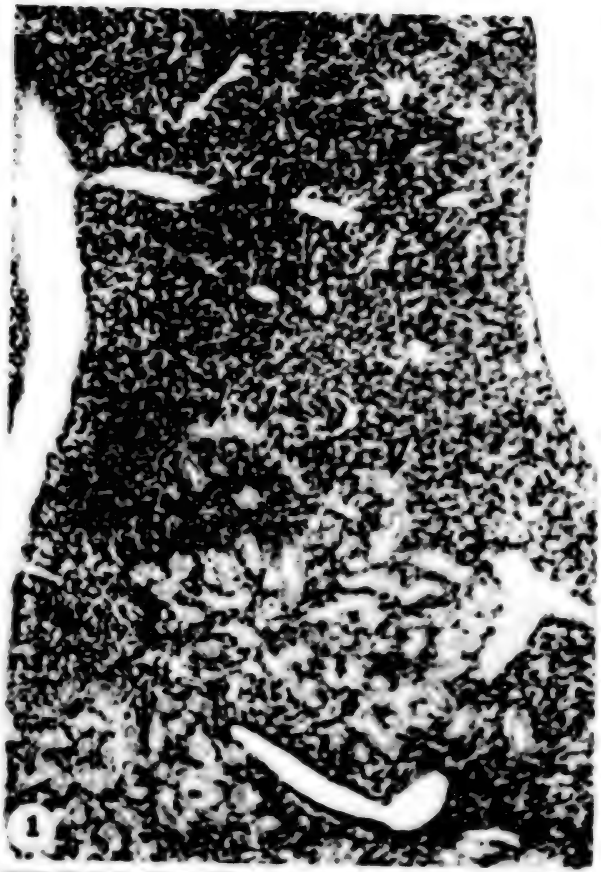
a. Afferent glomerular arteriole
b. Efferent glomerular arteriole
c. Glomerulus
d. Erythrocyte in glomerular capillary
e. Podocyte nucleus of the visceral epithelium of Bowman's capsule
f. Basement membrane of glomerulus
g. Squamous, parietal epithelium of Bowman's capsule
h. Bowman's space
i. Neck segment
j. First segment of proximal convoluted tubule
k. Brush border

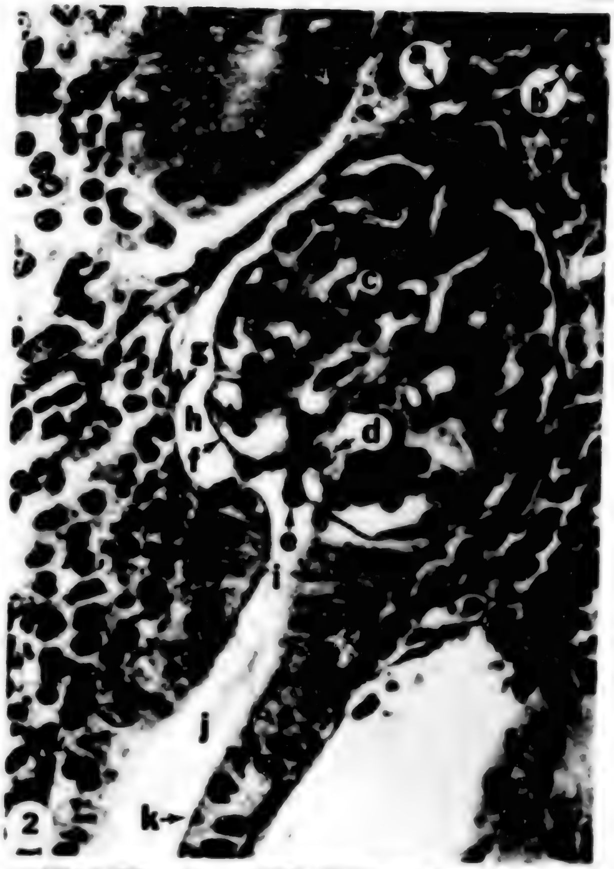
Fig. 3. Cross sections of the two morphologically distinct segments of the proximal tubule. ×700.

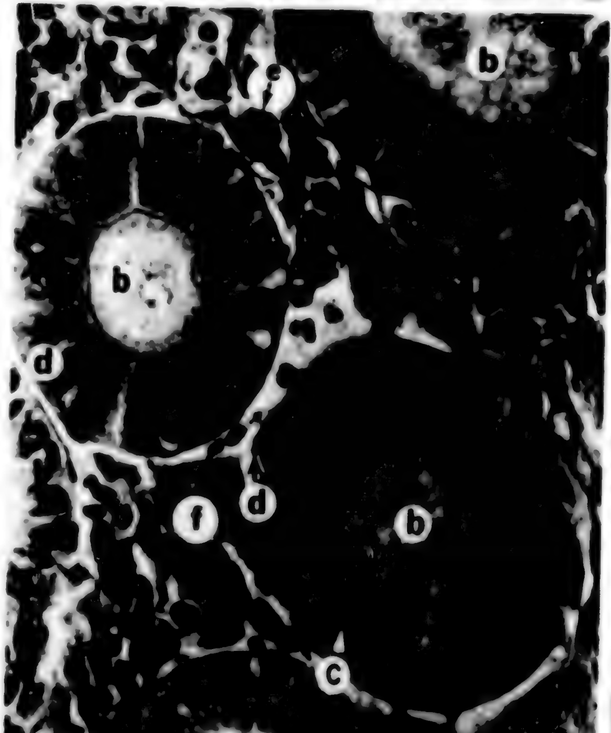
a. First segment of the proximal tubule
b. Second segment of the proximal tubule
c. Wandering lymphocyte
d. Nucleus of smooth muscle cell enveloping the tubule
e. Melanophore
f. Hematopoietic tissue

Fig. 4. Abrupt transition from the first segment to the second segment of the proximal tubule. ×700.

a. First segment of the proximal tubule
b. Second segment of the proximal tubule
c. Distal tubule


1


a
b
c
g
h
f
d
e
i
j
k
2


e
b
b
d
d
f
b
c
a
a
3

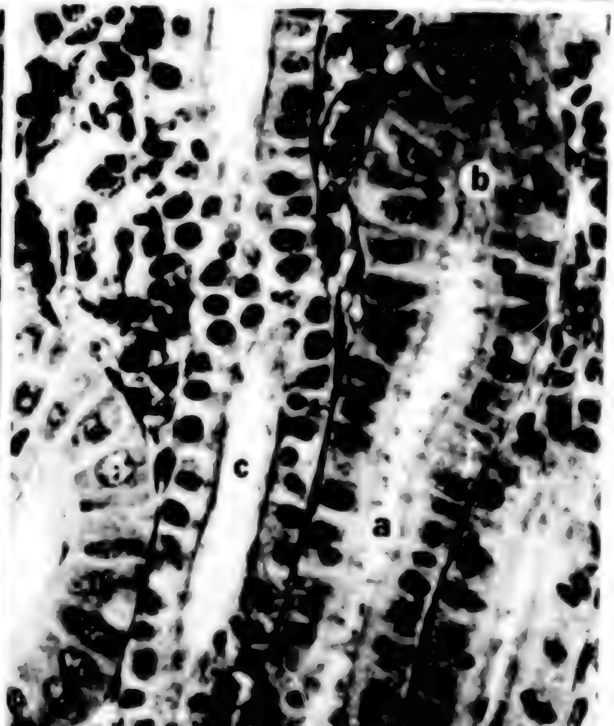

b
c
a
4

Plate 36. Kidney (2)

Fig. 1. Section of rainbow trout kidney, showing three major segments of the nephron. × 600.

a. First segment of the proximal tubule
b. Second segment of the proximal tubule
c. Distal tubule
d. Smooth muscle cell nucleus
e. Sinus containing various blood cells
f. Melanophore

Fig. 2. Longitudinal section, showing the abrupt transition from the second segment of the proximal tubule to the distal tubule. × 600.

a. Second segment of proximal tubule (dark staining)
b. Distal tubule (light staining region)
c. First segment proximal tubule

Fig. 3. Various tubule regions of normal trout kidney. × 225.

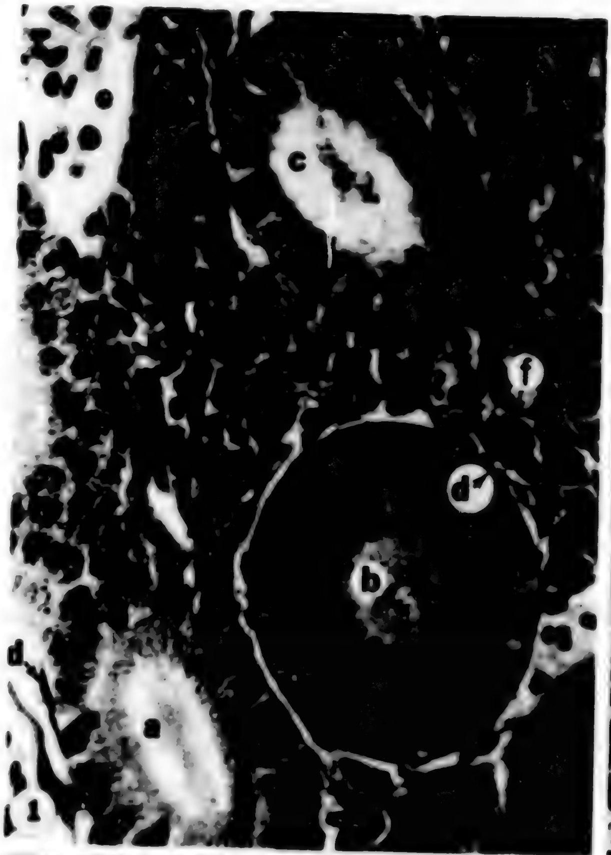
a. Second segment of the proximal tubule
b. Distal tubule
c. Collecting duct
d. Mesonephric duct
e. First segment of the proximal tubule
f. Blood sinus
g. Renal arterioles
h. Hematopoietic tissue

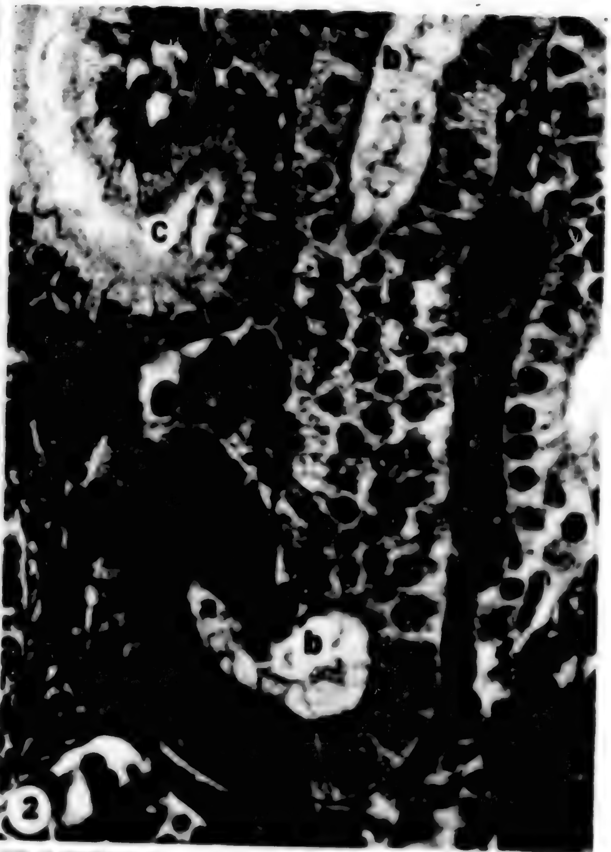
Fig. 4. Section of normal rainbow trout kidney, showing collecting duct entering the mesonephric duct. × 225.

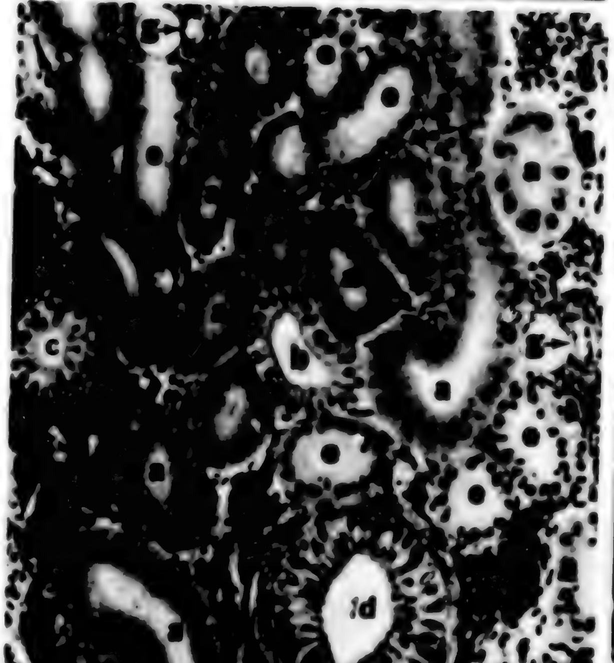
a. Collecting duct
b. Mesonephric duct
c. Connective tissue, which surrounds collecting ducts and mesonephric duct

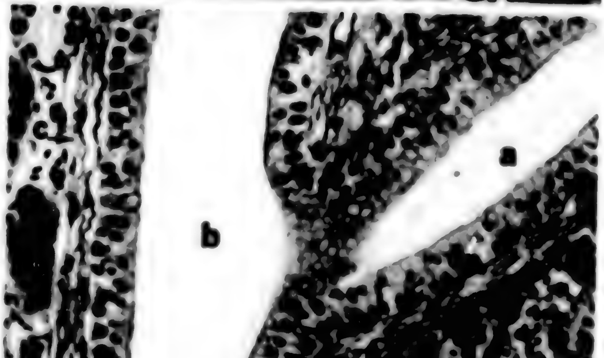
Fig. 5. An immature tubule (deeply basophilic) shown penetrating a collecting duct. (Tubules originate independently from the duct system and then penetrate and form a connection with a collecting duct, as shown here.) × 600.

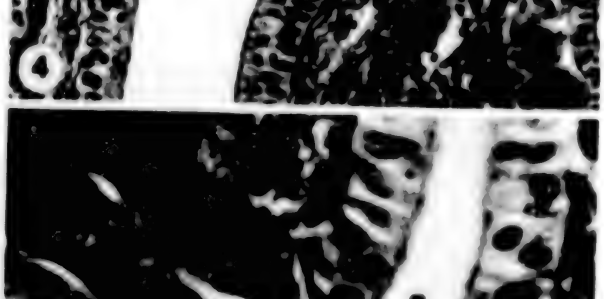
a. Collecting duct
b. Immature tubule


c
f
d
b
d
a
1


b
c
b
2


c
b
a
d
a
b
a
3


c
b
a
4


b
a
5

Chapter X

Nervous System

The nervous system of fish, like that of other vertebrates, is divided into two systems: the central system, consisting of the brain and spinal cord (central nervous system) and their respective nerves (peripheral nervous system); and the autonomic system, consisting of the nerves supplying the alimentary tract, swim bladder, urinogenital system, circulatory system, and other "involuntary" tissues.

The nervous system is also composed of two basic cell types, the neurons, and the neuroglial cells. The neurons conduct the nervous impulses and the neuroglial cells perform a supportive role. The neurons are composed of a cell body with the usual cellular components, as well as additional processes of many kinds. Usually several dendrites conduct impulses to the cell body, and one axon conducts the impulse away from the cell body. The dendritic processes of the neuronal cell body receive impulses from the sensory cells. The axon transmits the impulse to another neuron, or sometimes directly to the terminus – for example, a muscle. The "contacts" between neurons are called synapses. Much work has been done on the anatomy of synapses by light and electron microscopy (Bodian 1937; Gray 1961).

The neuroglial cells are of three distinct varieties (Kruger and Maxwell 1967): the ependymal cells, the astrocytes, and the oligodendrocytes. Ependymal cells line the ventricular and spinal canal, have cilia that project into the lumen of these cavities, and have long fibrillar processes that extend through the superimposed tissue to the pial surface. Astrocytes are said to be the most common of the neuroglial cells. They have many long processes that often surround and terminate at capillaries. Oligodendrocytes display occasional long processes, and their nuclei can be visualized by staining with hematoxylin and eosin. However, both the astrocytes and the oligodendrocytes, as well as the neuronal processes, are difficult or impossible to see in such preparations. These cells cannot be fully visualized without silver impregnation.

Brain

The unique arrangement of cellular types in the central nervous system of fish and other vertebrates is of interest to the neurohistologist. In this brief overview we consider that portion of the fish's brain known as the optic tectum, and list the several strata that compose it. Other portions of the brain also have their own characteristic architecture. At the surface of the optic lobe (Plate 37; Plate 38, Fig. 1), beneath the pia mater and dura mater, the first layer, the stratum marginale, is composed of unmyelinated fibers that run for long distances in a direction parallel to the surface of the optic tectum (Vanegas et al. 1974; Laufer and Vanegas 1974). This layer lacks cell bodies, and therefore appears relatively featureless, except for an occasional capillary. Layer 2, the stratum opticum, contains numerous myelinated axons of medium and large caliber; the tissue may be distinctly fibrous with scattered neuroglial cell nuclei (Plate 38). Layer 3, the stratum fibrosum et griseum superficiale, is made up of myelinated axons dispersed in all directions, and is interlaced horizontally and vertically by dendrites. Layer 4, the stratum griseum centrale, the broadest of the several layers, contains several kinds of neurons but is chiefly a synaptic neurophil that is visible only if it is "stained" by a silver technique. Layer 5, the stratum album centrale, is notable for its heavy fiber bundles. Layer 6, the stratum periventriculare, is another wide band of closely packed neuronal cell nuclei; beneath these nuclei are the nuclei of the ependymal cells that line the optic ventricle. From these ependymal cell bodies, long processes extend upward through all six layers and end just beneath the pial membrane (Schwassmann and Kruger 1968).

Certain other types of cells are conspicuous or have unusual functions. A pair of very large neurons in the medulla, called Mauthner cells (Plate 38, Fig. 5) have been the subject of extensive investigations and, because of their large size, it has been possible to elucidate their synaptic apparatus. Bodian (1937) described the axonic terminals of these cells by light microscopy, and Robertson et al. (1963) found by electron microscopy that the cell bodies are covered by a synaptic bed. Apparently the Mauthner cells function as muscle coordinators for relaying multiple sensory impulses mainly from lateral line centers to the caudal and abdominal swimming musculature (Lagler et al. 1977). Another large and conspicuous neuron is the Purkinje cell. In contrast to the single pair of Mauthner cells in the medulla, the Purkinje cells of the cerebellum are numerous (Plate 38, Fig. 2). The dendrites of these cells extend upward to the dorsal surface of the cerebellum and the axons project downward to the white matter beneath the granule cell layer. As previously mentioned, the two neuroglial cells – astrocytes and the oligodendrocytes – are similar in that their nuclei are the only parts that can be seen in hematoxylin and eosin preparations. The cytoplasm and the many long, arborescent processes cannot be seen unless they are impregnated with silver. Kruger and Maxwell (1967) discussed the comparative fine structure of these cells.

Spinal Cord

In the spinal cord the most prominent features are the cell bodies of the neurons, and the nuclei of the neuroglial cells, which stain deeply with hematoxylin. The gray fibrous material is referred to as the neurophil. Surrounding the central canal of the spinal cord are the ependymal cell bodies whose cilia extend into the lumen of the canal. In sections of the spinal cord these are vacuolated areas, each with a deeply stained nerve fiber. Originally the vacuolated area contained myelin, which is solvent extractable fat. Also in cross section may be seen the two Mauthner cell axons that extend from the medulla to the tip of the spinal cord (Plate 38, Fig. 5).

Ganglia (Plate 39) are characterized by very prominent nerve cell bodies and smaller nuclei of supporting cells. The nerves (Plate 39, Fig. 1) have a characteristic appearance, with elongated, deeply stained nuclei at intervals along the fibers. When a nerve is cut in cross section (Plate 39, Fig. 3), these nuclei appear round. Actually these axons are surrounded by an insulating myelin sheath and this sheath in turn is encased in a neurolemma. The nuclei of the neurolemma cells are deeply stained spindles (when cut longitudinally) or round bodies (when cross-sectioned). The myelin sheath, being fatty, is removed during tissue processing.

The neural tissues of fishes are fundamentally similar to those of mammals. Most of the cellular components of central and autonomic nervous systems of the trout have counterparts in the higher vertebrates, which closely resemble the corresponding components in the mammal.

Neurosecretory System

Neurosecretory cells in vertebrates are glandlike nerve cells located in widely separated areas of the central nervous system, but they are concentrated in the diencephalon. Fishes have, in addition, a caudal neurosecretory system, or urophysis, at the terminal end of the spinal cord (Plate 39; Kriebel 1980). The microscopic appearance of these cells is similar to that of the motor neurons, except that in the hypothalamus, the two types of neurons can be distinguished by their staining reaction. However, the Gomori staining procedure, which is suitable for the hypothalamus, does not serve to differentiate the neurosecretory cells of the caudal system (Bern 1969). Appropriate microscopic preparations will reveal droplets of colloidal material within the axon of the neurosecretory cells. These hormones or hormonal precursors travel from the neuron through the axon to its termination. Such terminations may be the cerebrospinal canal, or another neuron. It is presumed that the production of some or all of these neurosecretory cells is under nervous control. Their functional role is still not clear, but various investigators have suggested an ionoregulatory or osmoregulatory function, or both (Berlind 1973; Chevalier 1976; Kriebel 1980).

Specialized neurosecretory cells, known as Dahlgren cells, are found in the caudal region of the spinal cord of trout (Plate 40, Figs. 2 and 3). Their secretion is stored in a ventral enlargement (caudal neurosecretory system or urophysis) of the spinal cord near its posterior terminus (Bern 1969; Grizzle and Rogers 1976). The urophysial enlargement or sac is supported by a stroma of connective tissue and is filled with a large number of eosinophilic, secretory granules of a wide range of sizes. In addition, the sac contains capillaries and nerve fibers.

References

Ariens-Kappers, C. U., G. C. Huber, and E. C. Crosby. [1936] 1960. The comparative anatomy of the nervous system of vertebrates including man. Hafner Publishing Co., New York.

Aronson, L. R. 1967. Forebrain function in teleost fishes. Trans. N. Y. Acad. Sci. 29: 390–396.

Bartelmez, G. W., and N. L. Hoerr. 1933. The vestibular club endings in *Ameiurus*. Further evidence on the morphology of the synapse. J. Comp. Neurol. 57: 401–428.

Bauchot, R., R. Platel, J. M. Ridet, and M. Thireau. 1972. The brain of the rainbow trout *Salmo gairdneri* (Pisces, Teleostei, Salmonidae). Looking for a reference size for quantitative studies. Acta Zool. (Stockh.) 54: 53–64.

Beccari, N. 1920. Peculiara modalita nelle connessioni di alcuni neuroni del sistema nervoso centrale dei pesci. Arch. Ital. Anat. Embriol. 17: 239–283.

Berlind, A. 1973. Caudal neurosecretory systems: A physiologist's view. Am. Zool. 13: 759–770.

Bern, H. A. 1969. Urophysis and caudal neurosecretory system. Pages 399–418 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

Bern, H. A., and K. Lederis. 1969. A reference preparation for the study of active substances in the caudal neurosecretory system of teleosts. J. Endocrinol. 45: xi–xii.

Bern, H. A., and N. Takasugi. 1962. The caudal neurosecretory system of fishes. Gen. Comp. Endocrinol. 2: 96–110.

Bernstein, J. J. 1961*a*. Loss of hue discrimination in forebrain-ablated fish. Exp. Neurol. 3: 1–17.

Bernstein, J. J. 1961*b*. Brightness discrimination following forebrain ablation in fish. Exp. Neurol. 3: 297–306.

Bernstein, J. J. 1962. Role of the telencephalon in color vision in fish. Exp. Neurol. 6: 173–185.

Bernstein, J. J. 1970. Anatomy and physiology of the central nervous system. Pages 1–90 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 4. Academic Press, New York.

Best, A. C. G., and Q. Bone. 1973. The terminal neuromuscular junctions of lower chordates. Z. Zellforsch. Mikrosk. Anat. 143: 495–504.

Bodian, D. 1937. The structure of the vertebrate synapse. A study of the axon endings on Mauthner's cell and neighboring centers in the goldish. J. Comp. Neurol. 68: 117–159.

Bone, Q. 1963. The central nervous system. Pages 50–91 *in* A. Brodal and R. Fange, eds. Biology of myxine. Oslo University Press, Oslo.

Campbell, G. 1970. Autonomic nervous systems. Pages 109–132 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 4. Academic Press, New York.

Campbell, G., and B. J. Gannon. 1976. The splanchnic nerve supply to the stomach of the trout, *Salmo trutta* and *S. gairdneri*. Comp. Biochem. Physiol. C Comp. Pharmacol. 55:51–53.

Castejon, O. J., and A. J. Caraballo. 1980. Light and scanning electron microscopic study of cerebellar cortex of teleost fishes. Cell Tissue Res. 207: 211–226.

Chevalier, G. 1976. Ultrastructural changes in the caudal neurosecretory cells of the trout *Salvelinus fontinalis* in relation to external salinity. Gen. Comp. Endocrinol. 29: 441–454.

Clemente, C. D. 1964. Regeneration in the vertebrate central nervous system. Int. Rev. Neurobiol. 6: 257–301.

DeKock, L. L. 1963. A histological study of the head region of two salmonids with special reference to pressor- and chemo-receptors. Acta Anat. 55: 39–50.

Demski, L. S., and K. M. Knigge. 1971. The telencephalon and hypothalamus of the bluegill (*Lepomis macrochirus*): evoked feeding, aggressive and reproductive behavior with representative frontal sections. J. Comp. Neurol. 154: 1–16.

Demski, L. S., A. P. Evan, and L. C. Saland. 1975. The structure of the inferior lobe of the teleost hypothalamus. J. Comp. Neurol. 161: 483–498.

de Vlaming, V. L. 1975. Effects of pinealectomy on gonadal activity in the cyprinid teleost, *Notemigonus crysoleucas*. Gen. Comp. Endocrinol. 26: 36–49.

Dewsburg, S. A., and J. J. Bernstein. 1969. The role of the telencephalon in the performance of conditioned avoidance responses by goldfish. Exp. Neurol. 23: 445–456.

Diamond, J. 1971. The Mauthner cell. Pages 265–346 in W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 5. Academic Press, New York.

Enami, M. 1959. The morphology and functional significance of the caudal neurosecretory system of fishes. Pages 697–724 *in* A. Gorbman, ed. Comparative endocrinology. Wiley and Sons, New York.

Evans, A. P., L. S. Demski, and L. C. Saland. 1976. The lateral recess of the third ventricle in teleosts: An electron microscopic and Golgi study. Cell Tissue Res. 166: 521–530.

Fox, H., E. B. Lane, and M. Whitear. 1980. Sensory nerve endings and receptors in fish and amphibians. Pages 271–282 *in* R. I. C. Spearman and P. A. Riley, eds. The skin of vertebrates. Linnean Soc. Symp. Ser. 9. Dorset Press, Dorchester, Dorset.

Fridberg, G. 1962. Studies on the caudal neurosecretory system in teleosts. Acta Zool. (Stockh.) 43: 1–77.

Fridberg, G. 1963. Electron microscopy of the caudal neurosecretory system in *Leuciscus rutilus* and *Phoxinus phoxinus*. Acta Zool. (Stockh.) 44: 244–267.

Fridberg, G., and H. A. Bern. 1968. The urophysis and the caudal neurosecretory system of fishes. Camb. Philos. Soc. Biol. Rev. 43: 175–199.

Freihofer, W. C. 1966. The Sihler technique of staining nerves for systematic study especially of fishes. Copeia 1966: 470–475.

Frisch, von K. 1938. The sense of hearing in fish. Nature (Lond.) 141: 8–11.

Gray, E. G. 1961. Granule cells, mossy synapses and Purkinje spine synapses of the cerebellum: light and electron microscope observations. J. Anat. 95: 345–356.

Grizzle, J. M., and W. A. Rogers. 1976. Anatomy and histology of the channel catfish. Auburn University Agricultural Experiment Station, Auburn, Alabama. 94 pp.

Hill, J. J. 1968. The vascularization of the hypothalamic hypophyseal region of eastern brook trout *Salvelinus fontinalis*. Am. J. Anat. 122: 301–316.

Hinojosa, R. 1973. Synaptic ultrastructure in the tangential nucleus of the goldfish *Carassius auratus*. Am. J. Anat. 137: 159–186.

Honma, Y., and E. Tamura. 1967*a*. Studies on Japanese chars of the genus *Salvelinus*. III. The hypothalamohypophyseal vascular system of the Nikko-iwana, *Salvelinus leucomaenus pluvius*, in relation to its neurosecretory system. Bull. Jpn. Soc. Sci. Fish. 33: 303–310.

Honma, Y., and E. Tamura. 1967*b*. Studies on Japanese chars of the genus *Salvelinus*. IV. The caudal neurosecretory system of the Nikko-iwana *Salvelinus leucomenis pluvius* (Hilfendorf). Gen. Comp. Endocrinol. 9: 1–9.

Ito, H., and R. Kishida. 1975. Organization of the teleostean nucleus rotundus. J. Morphol. 147: 89–107.

Jansen, W. F., R. A. de Wager, R. A. Woutersen, H. van Loveren, and J. C. van de Kamer. 1976*a*. The saccus dorsalis of the rainbow trout, *Salmo gairdneri*: Richardson. Histological, cytochemical, electron microscopical, and autoradiographical observations. Cell Tissue Res. 167: 467–491.

Jansen, W. F., H. van Loveren, R. A. Woutersen, and R. A. de Wager. 1976*b*. Enzyme-cytochemistry of the saccus dorsalis of the rainbow trout, *Salmo gairdneri*: Richardson. Histochemistry 48: 233–306.

Karf, H. W. 1974. Acetylcholinesterase-positive neurons in the pineal and parapineal organs of the rainbow trout, *Salmo gairdneri*. Cell Tissue Res. 155: 475–490.

Kriebel, R. M. 1980. The caudal neurosecretory system of *Poecilia sphenops* (Poeciliidae). J. Morphol. 165: 157–165.

Kruger, L., and D. S. Maxwell. 1967. Comparative fine structure of vertebrate neuroglia: teleosts and reptiles. J. Comp. Neurol. 129: 115–142.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. R. M. Passino. 1977. Ichthyology, 2nd ed. John Wiley and Sons, New York. 506 pp.

Larsell, O. 1967. Teleostei. Pages 94–123 *in* J. Jansen, ed. The comparative anatomy and histology of the cerebellum from myxinids through birds. University of Minnesota Press, Minneapolis.

Laufer, M., and H. Vanegas. 1974. The optic tectum of a perciform teleost. II. Fine structure. J. Comp. Neurol. 154: 61–95.

Lederis, K. 1970. Active substances in the caudal neurosecretory system of bony fishes. Mem. Soc. Endocrinol. 18: 465–484.

Lederis, K. 1972. Recent progress in research on the urophysis. Gen. Comp. Endocrinol. Suppl. 3: 339–344.

Leghissa, S. 1955. La struttura microscopica e la ciloarchitettonica del tetto ottico dei placi Teleostei. Z. Anat. Entwicklungsgesch. 118: 427–463.

McNulty, J. A., and B. G. Nafpoktitis. 1977. Morphology of the pineal complex in seven species of lantern fishes (Pisces: Myctophidae). Am. J. Anat. 150: 509–530.

Moulton, J. M., and R. H. Dixon. 1967. Directional hearing in fishes. Pages 187–232 *in* W. N. Tavolga. Marine bioacoustics, vol. 2. Pergamon Press, Oxford.

Nieuwenhuys, R. 1962*a*. The forebrain of some groups of fishes. Anat. Rec. 142: 262. (Abstr.)

Nieuwenhuys, R. 1962*b*. Trends in the evolution of the actinopterygian forebrain. J. Morphol. 111: 69–88.

Nieuwenhuys, R. 1963. The comparative anatomy of the actinopterygian forebrain. J. Hirnforsch. 6: 171–192.

Nieuwenhuys, R. 1964. Comparative anatomy of the spinal cord. Prog. Brain Res. 11: 1–57.

Nieuwenhuys, R. 1967*a*. Comparative anatomy of olfactory centers and tracts. Prog. Brain Res. 23: 1–64.

Nieuwenhuys, R. 1967*b*. Comparative anatomy of the cerebellum. Prog. Brain Res. 25: 1–93.

Papez, J. W. [1929] 1967. Comparative neurology. Part 3, Chap. 37. Hafner Publishing Company, New York.

Pouweils, E. 1976. On the development of the cerebellum of the trout, *Salmo gairdneri*. Ph.D. Thesis. Catholic University, Nijmegen, Denmark.

Rao, P. D. P. 1967. Studies on the structural variations in the brain of teleosts and their significance. Acta Anat. 68: 379–399.

Reid, M. D., and R. A. Westerman. 1975*a*. Purkinje cell giant spikes in the trout *Salmo gairdneri* (Richardson). Comp. Biochem. Physiol. 50: 253–257.

Reid, M. D., and R. A. Westerman. 1975*b*. Visual responses in the cerebellum of the trout, *Salmo gairdneri* (Richardson). Comp. Biochem. Physiol. 50A: 259–262.

Retzlaff, E. 1957. A mechanism for excitation and inhibition of the Mauthner's cells in teleost: A histological and neurophysiological study. J. Comp. Neurol. 107: 209–225.

Reutter, K. 1974. Cholinergic innervation of scattered sensory cells in fish epidermis. Cell Tissue Res. 149: 143–146.

Rüdeberg, C. 1969. Structure of the parapineal organ of the adult rainbow trout, *Salmo gairdneri*, Richardson. Z. Zellforsch. Mikrosk. Anat. 93: 282–304.

Robertson, J. D., T. S. Bodenheimer, and D. E. Stage. 1963. The ultrastructure of Mauthner cell synapses and nodes in goldfish brains. J. Cell Biol. 19: 159–199.

Schnitzlein, H. N. 1962. The habenula and the dorsal thalamus of some teleosts. J. Comp. Neurol. 118: 225–267.

Schwartz, A. 1974. Metrische Untersuchunger zur Biomorphose der Mauthnerschen Zellen von *Salmo irideus* W. Gibb. Z. Mikrosk. Anat. Forsch. (Leipz.) 88: 257–272.

Schwassmann, H. O., and L. Kruger. 1965. Organization of the visual projection upon the optic tectum of some freshwater fish. J. comp. Neurol. 124: 113–128.

Schwassmann, H. O., and L. Kruger. 1968. Anatomy of visual centers in teleosts. Pages 1–16 *in* D. Ingle, ed. The central nervous system and fish behavior. University Chicago Press, Chicago.

Senn, D. G. 1976*a*. Brain structure in *Calamoichthys calabaricus* Smith 1865 (Polypteridae, Brachiopterygii). Acta Zool. (Stockh.) 57: 121–128.

Senn, D. G. 1976*b*. Notes on the midbrain and forebrain of *Calamoichthys calabaricus* Smith, 1865 (Polypteridae, Brachiopterygii). Acta Zool. (Stockh.) 57: 129–135.

Spath, M., and B. Lehmann. 1975. Structure and function of the neural connecting strands between the neuromasts of fish. J. Comp. Physiol. 103: 69–77.

Tuge, H., K. Uchihashi, and H. Shimamura. 1968. An atlas of the brains of fishes of Japan. Tsukiji Shokan Publ. Co. Ltd., Tokyo, Japan. 240 pp.

Vanegas, H., M. Laufer, and J. Amat. 1974. The optic tectum of a perciform teleost. I. General configuration and cytoarchitecture. J. Comp. Neurol. 154: 43–60.

von Bathelt, D. 1970. Experimentelle und vergleichend morphologische Untersuchungen am visuellen System von Teleosteirn. Zool. Jahrb. Abt. Anat. Ontognie Tiere 87: 402–470.

Watanabe, K. 1974. Banded spindle-shaped structures in the notochord of *Salmo irideus*. Anat. Rec. 178: 229–242.

Weis, J. S. 1968. Analysis of the development of the nervous system of the zebrafish *Brachydanio rerio*. I. The normal morphology and development of the spinal cord and ganglia of the zebrafish. J. Embryol. Exp. Morphol. 19: 109–119.

Whitear, M. 1952. The innervation of the skin of teleost fishes. Q. J. Microsc. Sci. 93: 289–305.

Whitear, M. 1971. Cell specialisation and sensory function in fish epidermis. J. Zool. (Lond.) 163: 237–264.

Wittenberg, J. B., and R. L. Holdrich. 1974. The choroid rete mirabile of the fish eye. II. Distribution and relation to the pseudobranch and to the swimbladder rete mirabile. Biol. Bull. (Woods Hole) 146: 137–156.

Wittenberg, J. B., and B. A. Wittenberg. 1974. The choroid rete mirabile of the fish eye. I. Oxygen secretion and structure: comparison with the swimbladder rete mirabile. Biol. Bull. (Woods Hole) 146: 116–136.

Yamauchi, A., and G. Burnstock. 1968. An electron microscope study on the innervation of the trout heart. J. Comp. Neurol. 132: 567–588.

Young, J. Z. 1935. The photo-receptors of lampreys. The function of the pineal complex. J. Exp. Biol. 12: 254–270.

Zottoli, S. J. 1978. Comparative morphology of the Mauthner cell in fish and amphibians. Pages 13–45 *in* D. Faber and H. Horn, eds. Neurobiology of the Mauthner cell. Raven Press, New York.

Plate 37. Central Nervous System

Fig. 1. Sagittal section of the brain of a 1-month-old rainbow trout. × 50.

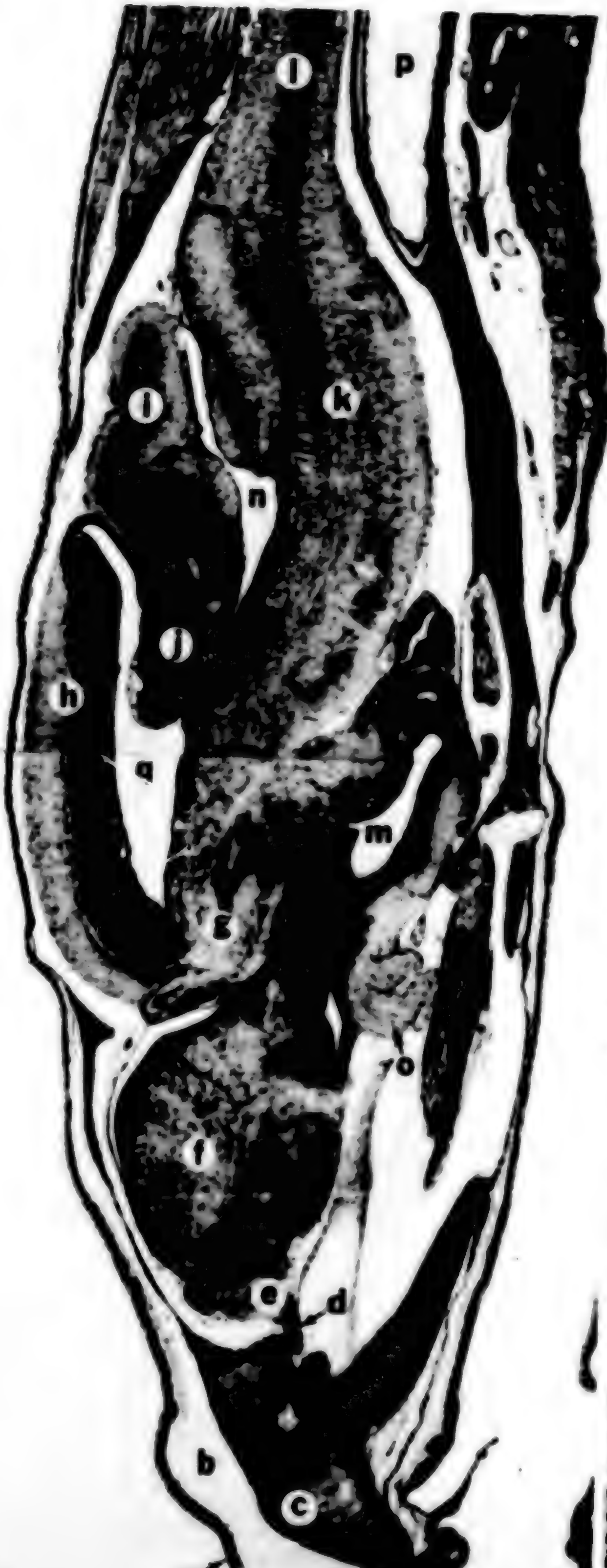
a. Epidermis
b. Mesenchymal tissue
c. Cartilage of the olfactory capsule
d. Portion of olfactory nerve
e. Olfactory lobe
f. Telencephalon (forebrain)
g. Diencephalon (between brain)
h. Mesencephalon (optic lobe)
i. Metencephalon (cerebellum)
j. Cerebellar valvula
k. Myelencephalon (medulla oblongata)
l. Spinal cord
m. 3rd ventricle
n. 4th ventricle
o. Optic nerve
p. Notochord

Fig. 2. Cross section of spinal cord of 3-month-old rainbow trout. × 300.

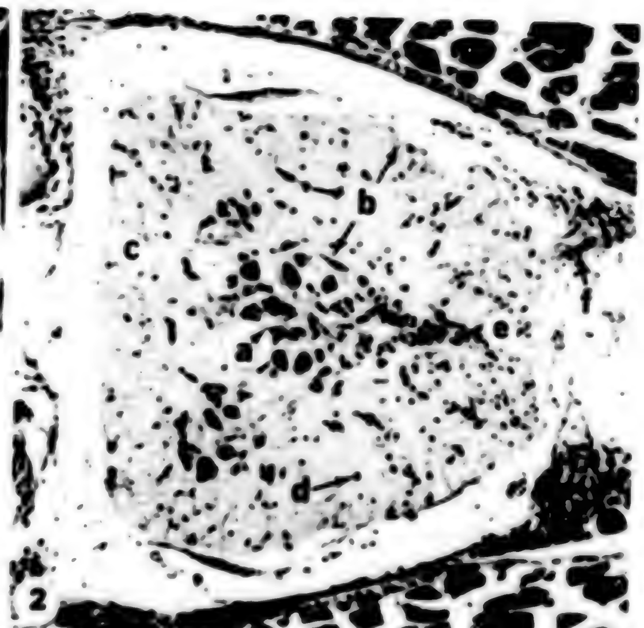
a. Neural canal
b. Gray matter (vertical horn)
c. White matter (myelinated nerve axons)
d. Nerve cell body
e. Gray matter (dorsal horn)

Fig. 3. Cross section of myelencephalon of 3-month-old rainbow trout at the level of the 10th (vagus) cranial nerve. × 200.

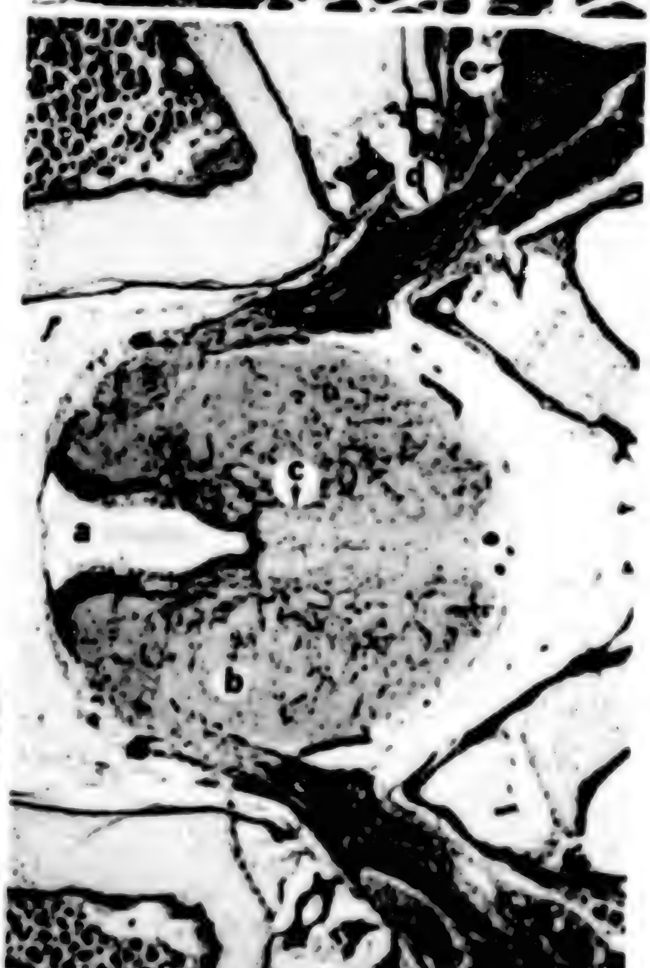
a. Dorsal fissure
b. Gray matter
c. White matter
d. Tenth cranial nerve (vagus)
e. Ganglion



1



2



3

Plate 38. Brain

Fig. 1. Sagittal section of the optic tectum of an 11-month-old rainbow trout. × 250.

a. Dura mater
b. Subarachnoid space
c. Pia mater, including many blood vessels
d. Stratum fibrosum marginale (molecular layer)
e. Stratum opticum
f. Stratum fibrosum et griseum superficiale
g. Stratum griseum centrale
h. Stratum album centrale
i. Stratum periventriculare (granular layer)

Fig. 2. Sagittal section of the cerebellum of 11-month-old rainbow trout. × 250.

a. Capillary
b. Molecular layer
c. Purkinje cell dendrites
d. Purkinje cell nuclei
e. Granular layer

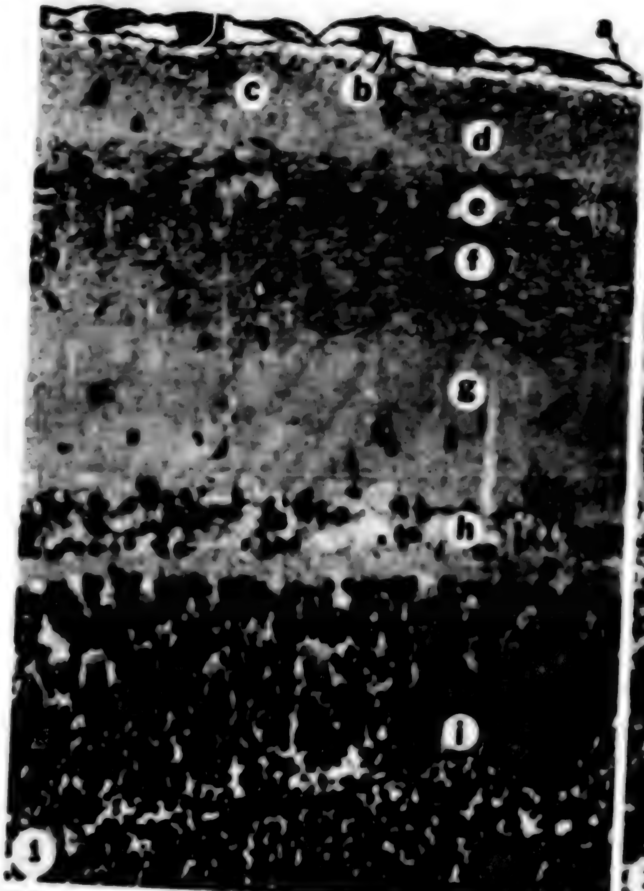
Fig. 3. Sagittal section of the cerebellar valvula of 11-month-old rainbow trout. × 250.

a. Granular layer
b. Molecular layer with Purkinje cell dendrites

Fig. 4. Sagittal section of the medulla of 11-month-old rainbow trout. × 250.

a. Giant nerve cell body in gray matter
b. Neuroglia cell nuclei in gray matter
c. White matter composed of nerve fiber tracts

Fig. 5. Detail of Mauthner cell. × 750. Masson's trichrome stain


a
c
b
d
e
f
g
h
i
1

a
b
c
b
d
e
2

a
b
3

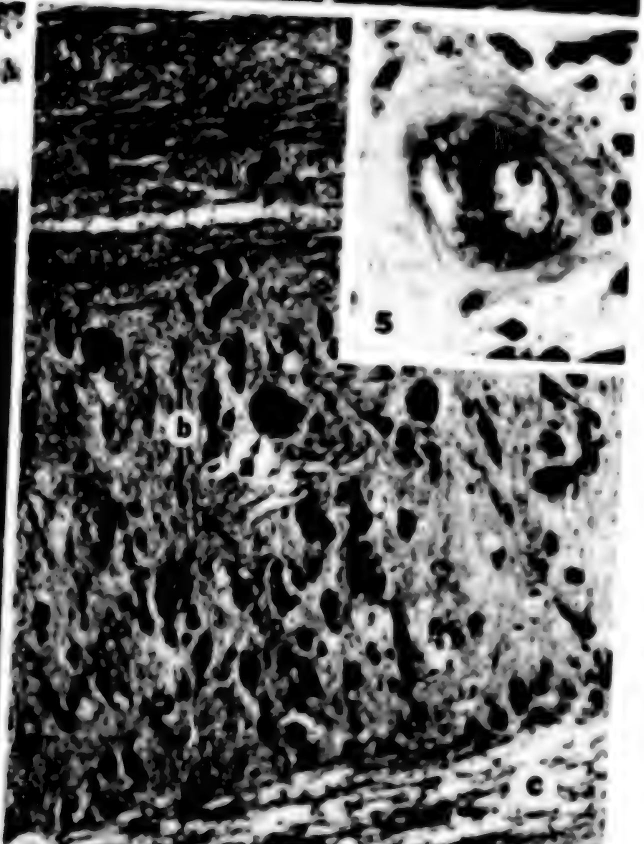

5
b
c
4

Plate 39. Nervous Tissue

Fig. 1. Fibers of the optic nerve of 3-month-old rainbow trout. × 750.

a. Nerve fibers

Fig. 2. Myelinated nerve fibers in the transverse septum of yearling rainbow trout. × 750.

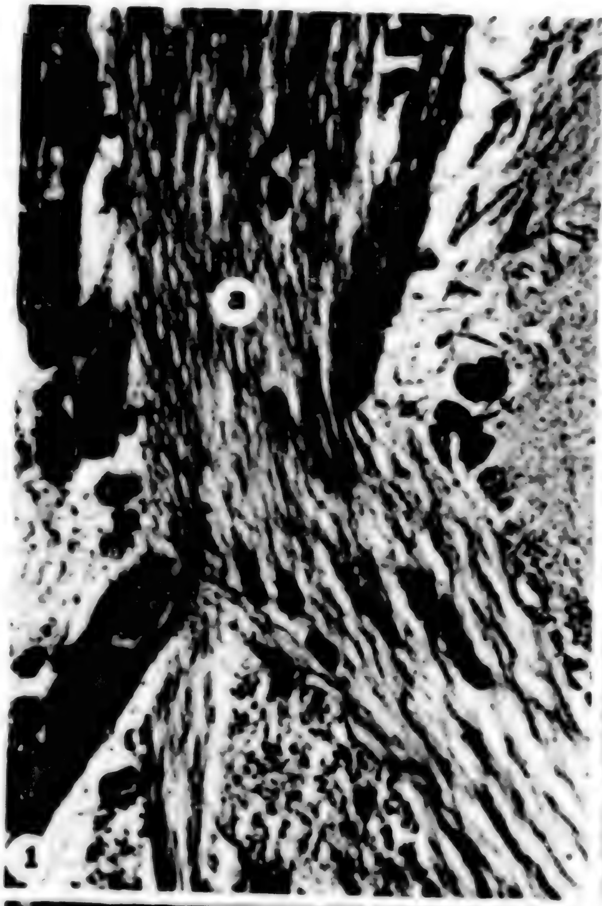
a. Nerve. Longitudinal section
b. Nerve. Cross section

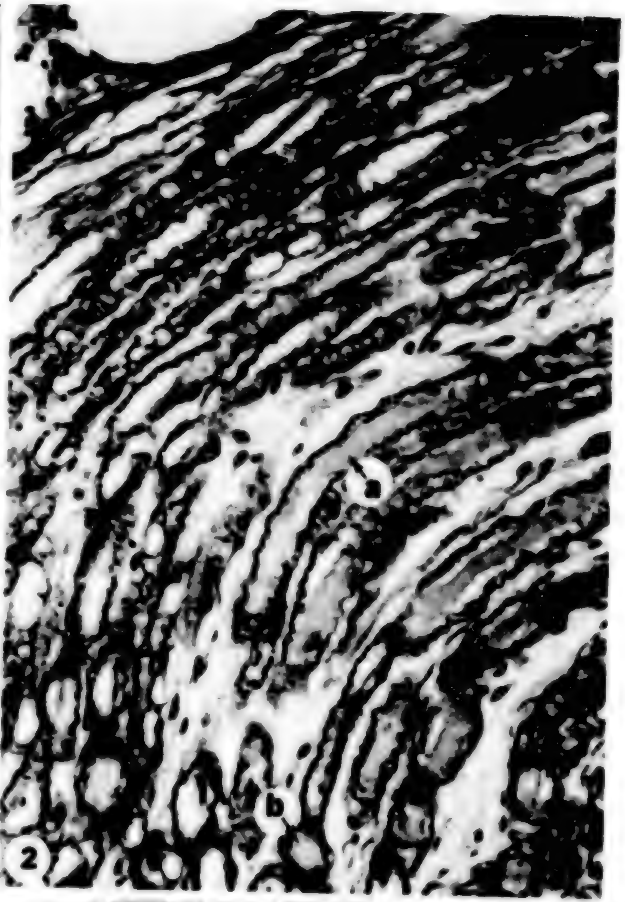
Fig. 3. Cross section of a cranial nerve surrounded by cranial cartilage. × 1200.

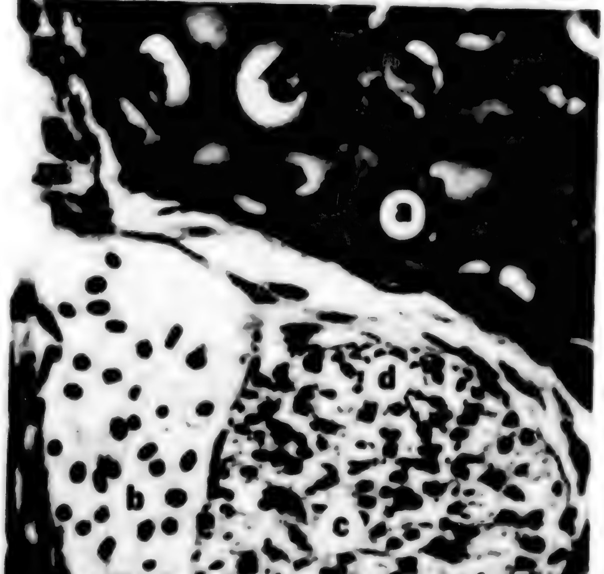
a. Cranial cartilage
b. Vein filled with erythrocytes
c. Cross section of nerve fascicle
d. Nuclei of neurolemma

Fig. 4. Portion of vagus nerve of 3-month-old rainbow trout. × 750.

a. Ganglion cell body
b. Nucleus of neurolemma (Schwann cell)


a
1


a
b
2


a
d
b
c
3

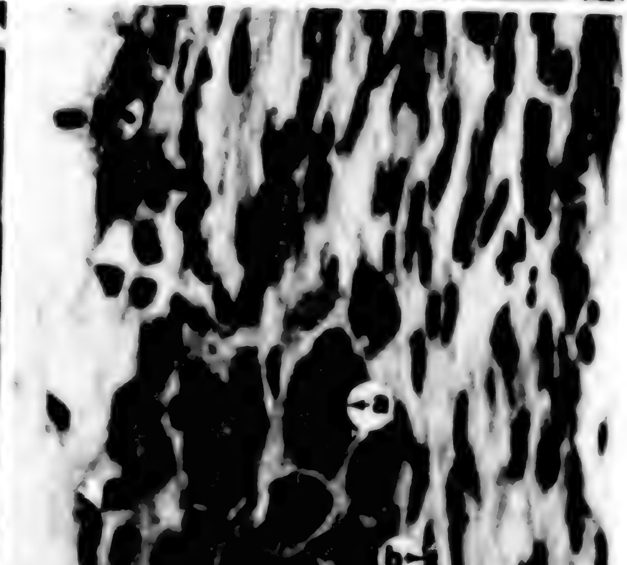

a
b
4

Plate 40. Caudal Neurosecretory Tissue (Urophysis)

Fig. 1. Sagittal section through the urophysis and spinal cord of yearling rainbow trout. × 40.

a. Urophysis
b. Spinal cord
c. Caudal neurosecretory Dahlgren cell

Fig. 2. Detail of Fig. 1. × 250.

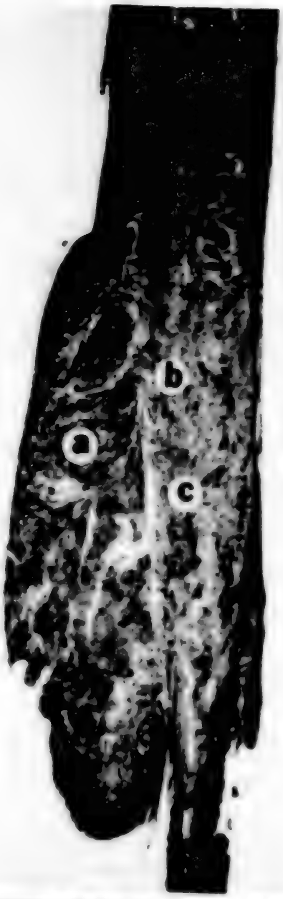
a. Dahlgren cell

Fig. 3. Detail of posterior end of gland shown in Fig. 1. × 250.

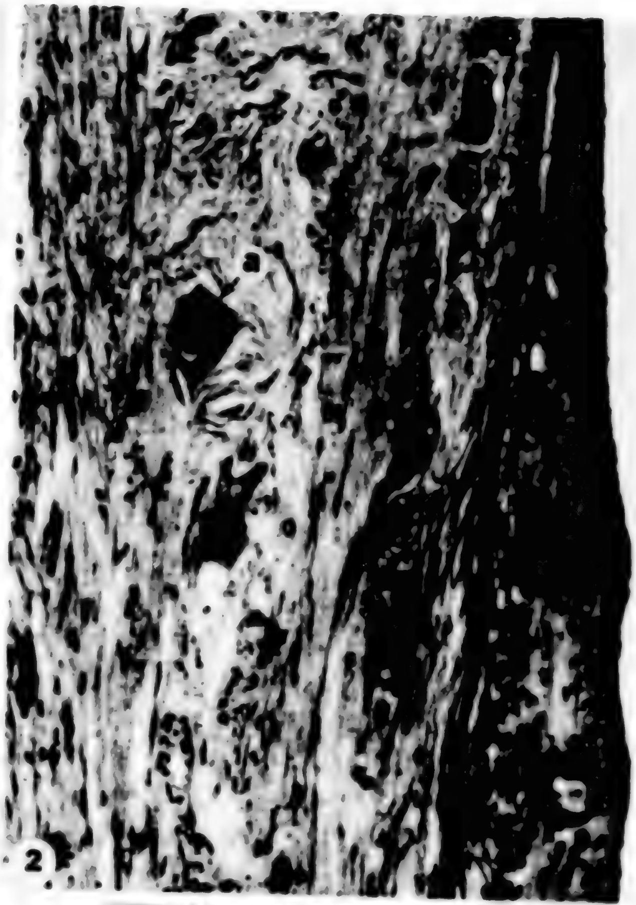
a. Granular secretory material
b. Dahlgren cell axons

Fig. 4. Detail of posterior portion of spinal cord. × 250.

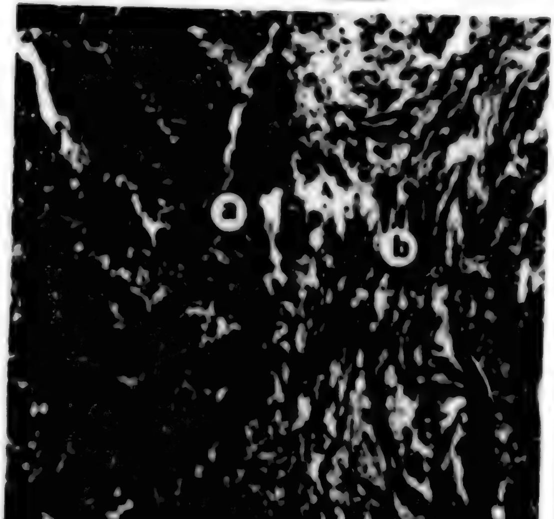
a. Dahlgren cell
b. Nerve fibers
c. Neuroglial cell nuclei



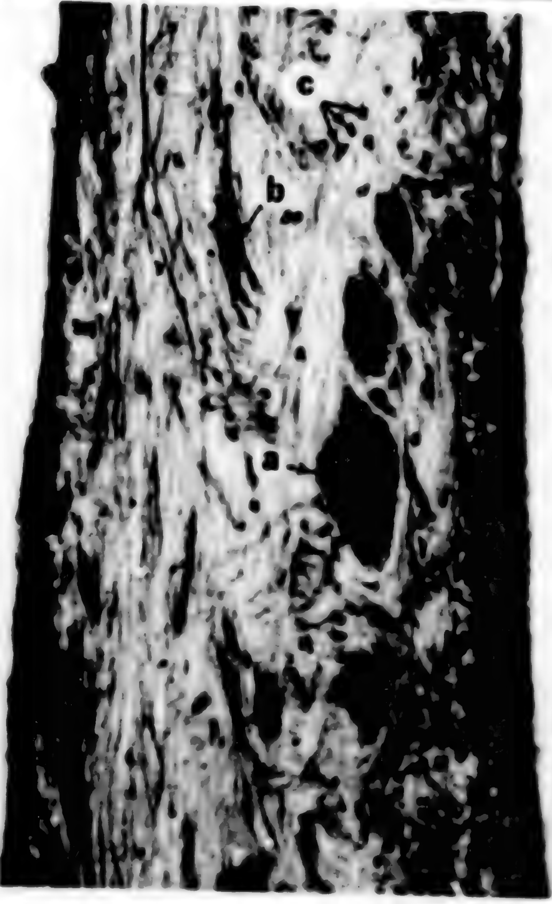
1



2



3



4

Blank Page

Chapter XI

Special Sensory Organs and Tissues

Optic Tissue

The retina is the most complex portion of the optic tissues, and that of salmonids has been the subject of many detailed histological reports (Brett and Ali 1958; Ali 1959, 1964, 1974; Jacquest and Beatly 1972; Pinganaud 1980; Khabibullina et al. 1981). It seems safe to assume that the retina in closely related fishes of the genus *Salmo* is not significantly different.

The retina is composed of eight layers (Plates 41 and 42). The pigmented epithelial layer (Plate 41, Fig. 3 and Plate 42) controls the amount of light reaching the visual elements beneath it; needlelike pigment granules are capable of migrating into fingerlike processes extending downward into the visual layer. The layer of rods and cones – also called the visual layer – consists of three types of receptors: twin cones, single cones, and rods. A single cone consists of three parts: the outer, the ellipsoid, and the myoid. The so-called outer sections extend upward into the pigmented epithelium, and the myoid portion extends downward into the rods and cones. The outer or external nuclear layer of rods and cones contains the nuclei of the visual rods and cones. The nuclei of the cones are large and spherical, whereas those of the rods tend to be small and oval. The outer plexiform layer contains darkly staining tips of rod and cone cells. The inner nuclear layer, as Brett and Ali (1958) pointed out, consists of bipolar cells, stellar ganglion cells, and amacrine cells. The inner plexiform layer consists of a broad layer of lightly staining reticular tissue and the axons of bipolar cells. The ganglion cell layer is composed of a narrow "chain of granular, spherical cells, with a surrounding reticular structure" (Brett and Ali 1958; Ali 1974). The nerve fiber layer consists of the nerve fibers leading to the optic tract.

The lens is a spherical ball consisting of three tissues. One consists of an encapsulating sheath of non-cellular transparent material, which is secreted by the second tissue, the underlying layer of physiologically active cells. The cells are nucleated and are capable of division and secretion. The third tissue, immediately beneath these active cells, and by far the greatest in volume, consists of the lens fibers (Plate 41, Fig. 5), which constitute most of the lens volume. These fibers are long, slender, transparent, non-nucleated cells lying in layers of long parallel rows. When the lens is dissected, these layers of cells resemble the layers of tissue in an onion. Each layer is one cell thick and is loosely cemented to the layer above and below it. In contrast to this method of attachment, the fibers of each layer are held to one another by a zipper-like interdigitation (Plate 41, Fig. 5). Whereas the mammalian lens is elastic, and can be modified in shape by contraction of the eye muscles, the fish lens is inelastic and must be drawn inward toward the retina by the retractor lentis muscle to accommodate changing sight requirements.

Olfactory Tissue

Salmonids and many other fishes have two nasal openings (Plate 43). In the grayling, *Thymallus arcticus*, a salmonid, water circulates through the olfactory apparatus as the fish swims (Watling and Hillemann 1964). This circulation also appears to occur in other salmonids. Watling and Hillemann (1964) described five cell types in a 3-month-old grayling olfactory epithelium, all of which can be assumed to be present in rainbow trout: neurosensory, ciliated columnar, mucous (or goblet), polygonal, and basal. Four of these can be identified in Plate 43, Fig. 4; the polygonal cell is the only one that cannot be clearly seen. The neurosensory cells, used in odor detection, are bipolar neurons. The cell body is located within the nuclear zone of the olfactory epithelium. The dendrite extends toward the surface, where it expands into a ciliated vesicle. The axon proceeds downward to penetrate the basement membrane. The typical ciliated columnar cell has its enlarged ciliated end reaching the surface and the opposite end tapering to a fine process. The mucous cells are less abundant and irregularly distributed. The basal cell rests on the lamina propria, and above it are several layers of polygonal cells containing spindle-shaped nuclei. Wandering lymphocytes and macrophages are frequently seen in various areas of the epithelium.

Gustatory Tissue

Taste buds or papillae are present in many parts of the buccal cavity and esophagus of trout (Plate 44). The sensory cells have filamentous extensions forming a characteristic "tuft," which projects from the sensory pit.

Sensory organs essentially like those in the mouth and esophagus occur on the surface of the trout head. It may be assumed that these also function in flavor discrimination.

Tactile organs or neuromasts are present in large numbers on the surface of the body and head of many larval fishes (Plate 45), and Sato (1955) believed them to be present in the pit organs of rainbow trout and chum salmon, *Oncorhynchus keta*. Except for the previously mentioned taste buds, we have been unable to find such sensory organs in larval rainbow trout. The differences between the tactile and the taste organs are real but not always easy to see microscopically. Whereas the hairlike extensions of the sensory cells of the tactile organs are covered by a gelatinous cupula, the taste organs have no such gelatinous covering. The refractory index of this cupula is close to that of water, making it difficult to observe the organs in life; and when they are processed for sectioning their structure is greatly altered.

Lateral Line Tissue

The most recent detailed morphological description of the salmonid lateral line system was published by Weber and Schiewe (1976). Valdykov (1926) and Disler (1960) also described these canals anatomically. The general morphology of the trunk lateral line canal, an expansion of Vladykov's concept as drawn by Weber and Schiewe (1976), is shown in Diagram 6. These investigators conceived of the trunk lateral line canal as a series of interconnecting chambers, each chamber being represented by a pocket in each lateral line scale. The two suprascalar and two infrascalar pores (Diagram 6a) lead into each lateral line scale pocket. Inasmuch as the scales overlap each other much like the shingles of a roof, communication between the scale pockets is by the posterior infrascalar pore of one scale lying over the anterior superscalar pore of the adjacent scale (Diagram 6b). The bilateral supraorbital, suborbital, preopercular-mandibular, and the temporal canals in the head region are continuous bilaterally with the canals of the trunk lateral line. The neuromasts in the head area are found in the skeletal portion just below the epidermis (Weber and Schiewe 1976).

Histologically, overlapping trout scales in cross section expose two scales and thus also expose two lateral line canals (Plates 46 and 47). Within the canal is at least one sensory organ. On the trout head there are many sensory pores, also part of the lateral line system. These pores permit water to enter and bring the sensory organs into intimate contact with the environment without exposing the delicate sensory cells to mechanical injury. Each neuromast is composed of a basal cluster of sensory cells and their supporting (sustentacular) cells. A group of filament-like processes, enclosed in the gelatinous cupula, project from these sensory cells.

Auditory Tissue

The auditory tissue of trout and many other fishes has four functions, as outlined by Lowenstein (1971): maintenance and regulation of muscle tone, maintenance of balance, gravity perception, and reception of sound. The labyrinth is in the posterior angles of the cranium, completely encased in cartilage and bone (Plate 48, Fig. 1). The structures involved are the semicircular canals and ampullae, which are filled with a fluid (endolymph). In addition, three ampullae – the utriculus, the sacculus, and the lagena – contain three calcareous stones or otoliths. The tissue of the canals and ampullae is a delicate "membrane" of connective tissue, which thickens as the fish matures until eventually it becomes rather tough. The sensory organ (Plate 48) is essentially like the sensory organs of the lateral line system, in which the sensory processes or filaments are covered by a cupula. The otoliths rest on the sensory hairs when the fish is in a normal, upright position; as this position is altered, the change in the gravitational force of the otoliths on the sensory hairs is the stimulus required for correction of a fish's orientation.

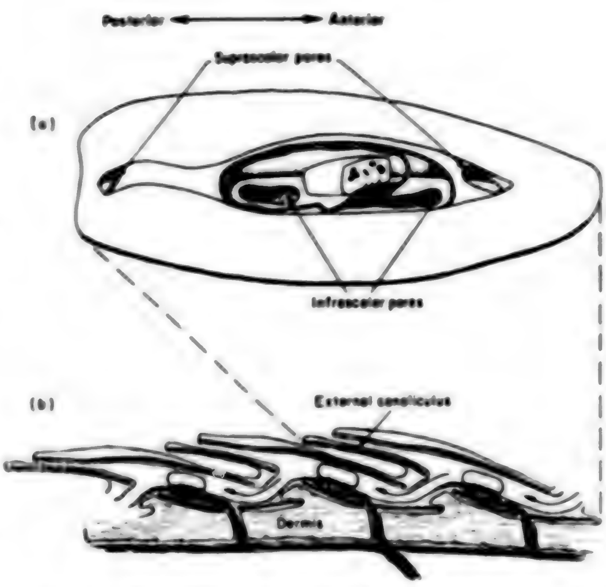


Diagram 6. (a) Lateral line scale with portion of dorsal surface removed to expose scale pocket and cross section of cupula and neuromast. (b) Longitudinal section through three lateral line scales. Lateral line canal is depicted by arrows. (From Weber and Schiewe 1976)

Pineal Organ

The pineal organ is anterior to the midbrain and dorsomedial to the forebrain (Plate 49). In most species of fish the organ is tubular or sac-shaped: the lumen is connected by an orifice to the third ventricle of the brain (Hafeez and Ford 1967). In young salmonids it is visible through the translucent cartilage of the cranial roof but in older fish this area becomes covered by ossification and heavily pigmented skin. It is generally believed that the organ is photosensitive, and presumably of greater importance to the younger trout. It has been shown that the pineal organ has a secretory function in some other species of fish. There is good reason to believe that the pineal has both photosensory and secretory functions (Dodt 1963; Falcon and Meissl

1981). However, the innervation of the organ has been difficult to trace, and further study will be needed before its physiological role is completely understood (Hafeez 1971).

Rodlet Cells

Rodlet cells (pyriform cells or "stabchendrusenzellen") have been observed, studied, and reported on by many histologists, beginning with Thelohan (1892). Their nature and function are still unclear and remain controversial (Modin 1981). Works of Leino (1974, 1979) and Flood et al. (1975) supported the belief that they are secretory cells. They have been found in many species of fish, including the salmonids, and are located in several tissues of the body, such as the heart, kidney, intestine, and gills.

Leino (1974, 1979) described the ultrastructure of both immature and mature rodlet cells. Under a light microscope the identifying features of these cells are the electron-dense, light refractory rods or spicules that extend from the interior (basal) end of the cell to the opening at the apex or exterior end of the cell (Plate 50). The maturing cell originates near the basal membrane of the epithelium and moves to the surface of the epithelium as it matures. Finally it appears to extrude (burst) its contents to the surface, whether it be the gill surface or the surfaces of internal organs.

Some researchers believe the rodlet cells to be parasites (Bannister 1966; Iwai 1968; Mourier 1970; Mayberry et al. 1979).

References

Optic Tissue

Ali, M. A. 1959. The ocular structure, retinomotor and photobehavioral responses of juvenile Pacific salmon. Can. J. Zool. 37: 965–996.

Ali, M. A. 1964. Retina of the albino splake (*Salvelinus fontinalis* × *S. namaycush*). Can. J. Zool. 42: 1158–1160.

Ali, M. A. 1974. Vision in fishes. Plenum Press, New York. 836 pp.

Ali, M. A., and M. Anctil. 1976. Retinas of fishes. Springer-Verlag, New York. 284 pp.

Ali, M. A., and M. Anctil. 1977. Retinal structure and function in the walleye (*Stizostedion vitreum vitreum*) and sauger (*S. canadense*). J. Fish. Res. Board Can. 34: 1467–1474.

Ali, M. A., R. A. Ryder, and M. Anctil. 1977. Photoreceptors and visual pigments as related to behavioral responses and preferred habitats of perches (*Perca* spp.) and pikeperches (*Stizostedion* spp.). J. Fish. Res. Board Can. 34: 1475–1480.

Anctil, M., and M. A. Ali. 1970. Retina of *Exocoetus volitans* and *Fodiator acutus* (Pisces, Exocoetidae). Copeia 1970: 43–48.

Arnott, H. J., A. C. G. Best, S. Ito, and J. A. C. Nicol. 1974. Studies on the eyes of catfishes with special reference to the tapetum lucidum. Proc. R. Soc. Lond. 186: 13–36.

Barnett, C. H. 1951. The structure and function of the choroidal gland of teleostean fish. J. Anat. 85: 113–119.

Braekevelt, C. R. 1974. Fine structure of the retinal pigment epithelium, Bruch's membrane, and choriocapillaris in the northern pike (*Esox lucius*). J. Fish. Res. Board Can. 31: 1601–1605.

Braekevelt, C. R. 1975. Photoreceptor fine structure in the northern pike (*Esox lucius*). J. Fish. Res. Board Can. 32: 1711–1721.

Braekevelt, C. R. 1980. Fine structure of the retinal pigment epithelium in the mud minnow (*Umbra limi*). Can. J. Zool. 58: 258–265.

Brett, J. R., and M. A. Ali. 1958. Some observations on the structure and photomechanical responses of the Pacific salmon retina. J. Fish. Res. Board Can. 15: 815–829.

Bridges, C. D. B. 1956. The visual pigments of the rainbow trout *Salmo irideus*. J. Physiol. 134: 620–629.

Bridges, C. D. B., and S. Yashikami. 1970. Distribution and evaluation of visual pigments in salmonid fishes. Vision Res. 10: 609–626.

Copeland, D. E. 1974*a*. The anatomy and fine structure of the eye in teleost. I. The choroid body in *Fundulus grandis*. Exp. Eye Res. 18: 547–561.

Copeland, D. E. 1974*b*. The anatomy and fine structure of the eye in teleost. II. The vascular connections of the lentiform body in *Fundulus grandis*. Exp. Eye Res. 19: 583–589.

Copeland, D. E. 1976. The anatomy and fine structure of the eye in teleost. IV. The choriocapillaris and the dual vascularization of the area centralis in *Fundulus grandis*. Exp. Eye Res. 22: 169–179.

Copeland, D. E. 1982. The anatomy and fine structure of the eye in fish. VI. Ciliary type tissue in nine species of teleosts. Biol. Bull. 163: 131–143.

Copeland, D. E., and D. S. Brown. 1976. The anatomy and fine structure of the eye in teleosts. V. Vascular relations of choriocapillaris, lentiform body and falciform process in rainbow trout (*Salmo gairdneri*). Exp. Eye Res. 23: 15–27.

Copeland, D. E., and A. T. Fitzjarrell. 1975. The anatomy and fine structure of the eye in teleost. III. The structure of the lentiform body in *Fundulus grandis*. Exp. Eye Res. 21: 515–521.

Edelhauser, H. F. 1968. Ultrastructure of trout cornea. J. Fish. Res. Board Can. 25: 863–866.

Engstrom, K. 1960. Cone types and cone arrangement in the retina of some cyprinids. Acta Zool. (Stockh.) 41: 277–295.

Engstrom, K. 1962. Cone types and cone arrangements in teleost retinae. Acta Zool. (Stockh.) 44: 179–243.

Engstrom, K. 1963. Structure, organization and ultrastructure of the visual cells in the teleost family, Labridae. Acta Zool. (Stockh.) 44: 1–41.

Harding, C. V. 1973. Corneal epithelial surfaces in elasmobranchs and teleosts as seen with the scanning electron microscope. Biol. Bull. (Woods Hole) 5: 345–351.

Jacquest, W. L., and D. D. Beatly. 1972. Visual pigment changes in the rainbow trout, *Salmo gairdneri*. Can. J. Zool. 50: 1117–1126.

Johns, P. R. 1981. Growth of fish retinas. Am. Zool. 21: 447–458.

Khabibullina, L. A., R. D. Khabibullina, A. S. Stepanov. 1981. The structure of eye and retina in the pink salmon, *Oncorhynchus gorbuscha*. Zool. Zh. 60: 725.

Kruger, L., and D. S. Maxwell. 1966. The fine structure of ependymal processes in the teleost optic tectum. Am. J. Anat. 119: 479–488.

Lagler, K. F., J. E. Bardach, R. R. Miller, and D. R. M. Passino. 1977. Ichthyology, 2nd ed. John Wiley & Sons, Inc., New York. 506 pp.

Lyall, A. H. 1957*a*. The growth of the trout retina. Q. J. Microsc. Sci. 98: 101–110.

Lyall, A. H. 1957*b*. Cone arrangement in teleost retinae. Q. J. Microsc. Sci. 98: 189–210.

Mung, E. W., and D. D. Beatly. 1965. A critical analysis of the visual pigments of salmon and trout. Vision Res. 5: 1–17.

Nicol, J. A. C. 1980. Guanine in strata argente of fish eyes. Can. J. Zool. 58: 488–492.

Nicol, J. A. C., and H. J. Arnott. 1973. Studies on the eyes of gars, Lepisosteidae, with special reference to the tapetum lucidum.

Can. J. Zool. 51: 501-508.

Payrau, P., G. Offret, J. P. Faure, Y. Pouliquen, and G. Cuq. 1964. On the lamellar structure of the corneas of certain fishes. Arch. Ophthalmol. 24: 685-690.

Pinganaud, G. 1980. Development of the trout visual system (*Salmo irideus*). Arch. Anat. Microsc. Morphol. Exp. 69: 215-231.

Schuster, T. 1971. Beitrag zur Architektonik der Riesensynapsen in Nucleus narvi oculomotorii bei *Salmo trutta irideus*. Z. Mikrosk. Anat. Forsch. (Leipz.) 83: 518–524.

Schuster, T., and H. Leotzke. 1971. Cytoarchitektonid und biomorphose des nc. n. oculomotorii bei *Salmo trutta irideus*. Z. Mikrosk. Anat. Forsch. (Leipz.) 83: 246-276.

Stell, W. K. 1972. The structure and morphologic relations of rods and cones in the retina of the spiny dogfish, *Squalus*. Comp. Biochem. Physiol. 42A: 141-151.

Stell, W. K., and P. Witkovsky. 1973*a*. Retinal structure in the smooth dogfish, *Mustelus canis:* Light microscopy of photoreceptor and horizontal cells. J. Comp. Neurol. 148: 33-46.

Stell, W. K., and P. Witkovsky. 1973*b*. Retinal structure in the smooth dogfish, *Mustelus canis:* General description and light microscopy of giant ganglion cells. J. Comp. Neurol. 148: 1–32.

Vanegas, H., and S. O. E. Ebbesson. 1973. Retinal projections in the perch-like teleost *Eugerres plumieri*. J. Comp. Neurol. 151: 331-358.

Vanegas, H., M. Laufer, and J. Amat. 1974. The optic tectum of a perciform fish. I. General configuration and cytoarchitecture. J. Comp. Neurol. 154: 43-60.

Watanabe, Y., and J. Yamada. 1980. Histological characteristics of cataractous eye lenses in cultured masu salmon. Bull. Fac. Fish. Hokkaido Univ. 31: 290-296.

Witkovsky, P., and W. K. Stell. 1973. Retinal structure in the smooth dogfish, *Mustelus canis:* light microscopy of bipolar cells. J. Comp. Neurol. 148: 47-60.

Olfactory Tissue

Bannister, L. H. 1965. The fine structure of the olfactory surface of teleostean fishes. Q. J. Microsc. Sci. 106: 332-342.

Bertmar, G. 1972*a*. Labyrinth cells, a new cell type in vertebrate olfactory organs. Z. Zellforsch. Mikrosk. Anat. 132: 245-256.

Bertmar, G. 1972*b*. Ecostructural studies on olfactory organ in young and adult sea trout. Z. Morphol. Tiere 72: 307–330.

Bertmar, G. 1972*c*. Scanning electron microscopy of olfactory rosette in sea trout. Z. Zellforsch. Mikrosk. Anat. 128: 336–346.

Bertmar, G. 1973. Ultrastructure of the olfactory mucosa in the homing Boltis sea trout *Salmo trutta trutta*. Marine Biol. 19: 74–88.

Breipohl, W., G. J. Bijvank, and H. P. Zippel. 1973. Scanning electron microscopy of olfactory receptors in *Carassius auratus*. Z. Zellforsch. Mikrosk. Anat. 138: 439–454.

Caprio, J., and R. Raderman-Little. 1978. Scanning electron microscopy of the channel catfish olfactory lamellae. Tissue & Cell 10: 1–9.

Gemne, G., and K. B. Dving. 1969. Ultrastructural properties of primary olfactory neurons in fish. Am. J. Anat. 126: 457–476.

Hall, A., E. Schulte, and W. Holl. 1971. Crossing-over of olfactory fiber bundles within the olfactory bulb of catfishes. Z. Naturforsch. Sect. B. 26: 739–740.

Ichikawa, M., and K. Ueda. 1979. Electron microscopic study of the termination of the centrifugal fibers in the goldfish olfactory bulb. Cell Tissue Res. 197: 257–262.

Jahn, L. A. 1972. Development of the olfactory apparatus of the cutthroat trout. Trans. Am. Fish. Soc. 101: 284-289.

Johns, P. R. 1977. Growth of the adult goldfish eye. III. Source of the new retinal cells. J. Comp. Neurol. 176: 343–357.

Johns, P. R., and S. S. Easter. 1977. Growth of the adult goldfish eye. II. Increase in retinal cell number. J. Comp. Neurol. 176: 331–342.

Kapoor, A. S., and P. P. Ojha. 1973*a*. The olfactory apparatus in the flatfish, *Cynoglossus oligolepis*. Trans. Am. Microsc. Soc. 92: 298–304.

Kapoor, A. S., and P. P. Ojha. 1973*b*. Histology of the olfactory epithelium of the fish *Channa punctatus* Bloch. Acta Anat. 87: 534–554.

Kleerkoper, H. 1969. Olfaction in fishes. Indiana University Press, Bloomington. 222 pp.

Lowe, G. A., and N. K. MacLeod. 1975. The ultrastructural organization of olfactory epithelium of two species of gadoid fish. J. Fish Biol. 7: 529–532.

Pfiffer, W. 1963. The morphology of the olfactory organ of the Pacific salmon *Oncorhynchus*. Can. J. Zool. 41: 1233–1236.

Sheldon, R. E. 1912. The olfactory tracts and centers in teleosts. J. Comp. Neurol. 22: 177–340.

Sutterlin, A. M., and N. Sutterlin. 1971. Electrical responses of the olfactory epithelium of Atlantic salmon *Salmo salar*. J. Fish. Res. Board Can. 28: 565–572.

Takagi, S. F. 1965. Electrical activity and histological change in the degenerating olfactory epithelium. J. Gen. Physiol. 48: 559–569.

Theisen, B. 1976. The olfactory system in the Pacific hagfishes *Eptatretus stoutii*, *Eptatretus deani*, and *Myxine circifrons*. Acta Zool. (Stockh.) 57: 167–173.

Verraes, W. 1976. Postembryonic development of the nasal organs, sacs and surrounding skeletal elements in *Salmo gairdneri* (Teleostei: Salmonidae), with some functional interpretations. Copeia 1976: 71–75.

Watling, H., and H. H. Hillemann. 1964. The development of the olfactory apparatus of the grayling *Thymallus arcticus*. J. Fish. Res. Board Can. 21: 373–396.

Zeiske, E. 1973. Morphologische Untersuchungen am Geruchsorgan von Zahnkarpfen (Pisces, Cyprinodontoidia). Z. Morphol. Tiere 74: 1–16.

Gustatory Tissue

Ezeasor, D. N. 1982. Distribution and ultrastructure of taste buds in the oropharyngeal cavity of the rainbow trout, *Salmo gairdneri* Richardson, during fasting. J. Fish Biol. 20: 53–68.

Fujiya, M., and J. E. Bardach. 1966. A comparison between the external taste sense of marine and freshwater fishes. Bull. Jpn. Soc. Sci. Fish. 32: 45–56.

Herrick, C. J. 1904. The organ and sense of taste in fishes. Bull. U.S. Fish. Comm. 22: 239–272.

Hidaka, I., and S. Yokota. 1967. Taste receptor stimulation by sweet-tasting substances in the carp. Jpn. J. Physiol. 17: 652–666.

Hirata, Y. 1966. Fine structure of the terminal buds on the barbels of some fishes. Arch. Histol. Jpn. 26: 507–523.

Hoagland, H. 1933. Specific nerve impulses from gustatory and tactile receptors in catfish. J. Gen. Physiol. 16: 685–693.

Konishi, J., and H. Niwa. 1964. Some properties of taste receptors in freshwater fish: Responses to weak solutions. Jpn. J. Physiol. 14: 328–343.

Konishi, J., and Y. Zotterman. 1963. Taste functions in fish. Pages 215–233 *in* Y. Zotterman, ed. Olfaction and taste. MacMillan, New York.

Reutter, K. 1973. Typisierung der Geschmacksknospen von Fischen. I. Morphologische und neurohistochemische Untersuchungen an *Xiphophorus helleri* Heckel (Poeiliidae, Cyprinodontiforme, Teleostei). Z. Zellforsch. Mikrosk. Anat. 143: 409–423.

Reutter, K. 1974. Taste bud types in fishes. II. Scanning electron microscopical investigations on *Xiphophorus helleri* Heckel

(Poeciliidae, Cyprinodontiformes, Teleostei). Cell Tissue Res. 153: 151–165.

Sato, M. 1955. Studies on the pit organs of fishes. I. Histological structure of the large pit organs. Jpn. J. Zool. XI: 443–452.

Scharrer, E., S. W. Smith, and S. L. Palay. 1947. Chemical sense and taste in the fishes, *Prionotus* and *Trichogaster*. J. Comp. Neurol. 86: 183–198.

Whitear, M. 1965. Presumed sensory cells in fish epidermis. Nature (Lond.) 208: 703–704.

Lateral Line Tissue

Allis, E. P., Jr. 1905. The latero-sensory canals and related bones in fishes. Int. Monatsschr. Anat. Physiol. 21: 401–503.

Alnaes, E. 1973. Two types of lateral line afferents in the eel (*Anguilla anguilla*). Acta Physiol. Scand. 87: 535–548.

Andrianov, G. N., and O. B. Ilyinsky. 1973. Some functional properties of central neurons connected with the lateral-line organs of the catfish (*Ictalurus nebulosus*). J. Comp. Physiol. 86: 365–376.

Bailey, S. W. 1937. An experimental study of the origin of lateral line structures in embryonic and adult teleosts. J. Exp. Zool. 76: 187–233.

Bennett, M. V. L. 1967. Mechanisms of electroreception. Pages 313–393 *in* P. Cahn, ed. Lateral line detectors. Indiana University Press, Bloomington.

Bennett, M. V. L. 1971. Electroreception. Pages 493–574 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology. vol. 4. Academic Press, New York.

Branson, B. A., and G. A. Moore. 1962. The lateralis components of the acoustico-lateralis system in the sunfish family, Centrarchidae. Copeia 1962: 1–108.

Cahn, P. H., and E. Shaw. 1962. The first demonstration of lateral line cupulae in the Mugiliformes. Copeia 1962: 109–114.

Denny, M. 1937. The lateral line system of the teleost, *Fundulus heteroclitus*. J. Comp. Neurol. 68: 49–65.

Dijkgraaf, S. 1962. The functioning and significance of the lateral-line organs. Biol. Rev. Camb. Philos. Soc. 38: 51–105.

Dijkgraaf, S. 1968. Electroreception in the catfish *Amiurus nebulosus*. Experientia (Basel) 24: 187–188.

Disler, N. N. 1960. Organy chuvstv sistemy bokovoi linii i ikh znachneie povedenii ryb. [Lateral line sense organs and their importance in fish behavior.] Izd. Akad. Nauk SSSR. 310 pp. (Transl. by Israel Program Sci. Transl., 1971, available from Natl. Tech. Inf. Serv., Springfield, Va., as TT 70-54021.)

Disler, N. N., and S. A. Smirnov. 1977. Sensory organs of the lateral-line canal system in two percids and their importance in behavior. J. Fish. Res. Board Can. 34: 1492–1503.

Enin, L. D., and O. B. Ilyinsky. 1972. Representation of the lateral-line nerves in the cerebellum of skates. Nejirofiziologia 4: 192–200. [In Russian]

Flock, A. 1965. Electron microscopic and electrophysiological studies on the lateral line canal organ. Acta Oto-Laryngol. (Suppl.) 199: 1–90.

Flock, A. 1967. Ultrastructure and function in the lateral line organs. Pages 163–197 *in* P. H. Cahn, ed. Lateral line detectors. Indiana University Press, Bloomington.

Flock, A., and J. Wersall. 1962*a*. A study of the orientation of the sensory hairs of the receptor cells in the lateral line organ of fish, with special reference to the function of the receptors. J. Cell Biol. 15: 19–27.

Flock, A., and J. Wersall. 1962*b*. Synaptic structures in the lateral line canal organ of the teleost fish *Lota vulgaris*. J. Cell Biol. 13: 337–343.

Hama, K. 1965. Some observations on the fine structure of the lateral line organ of the Japanese sea eel *Lyncozymba nystromi*. J. Cell Biol. 24: 193–210.

Hashimoto, T., Y. Katsuki, and K. Yanagisawa. 1970. Efferent system of lateral-line organ of fish. Comp. Biochem. Physiol. 33: 405–421.

Hoss, D. E., and J. H. S. Blaxter. 1982. Development and function of the swimbladder-inner ear-lateral line system in the Atlantic menhaden, *Brevoortia tyrannus* (Latrobe). J. Fish Biol. 20: 131–142.

Hoyt, R. D. 1972. Anatomy and osteology of the cephalic lateral-line system of the silverjaw minnow, *Ericymba buccata* (Pisces: Cyprinidae). Copeia 1962: 812–816.

Iwai, T. 1967. Structure and development of lateral line cupulae in teleost larvae. Pages 27–44 *in* P. H. Cahn, ed. Lateral line detectors. Indiana University Press, Bloomington.

Jakubowski, M. 1965. Cutaneous sense organs of fishes. II. The structure of lateral line organs in the burbot *Lota lota* L. and pike *Esox lucius* L. Acta Biol. Cracov. Ser. Zool. 8: 87–99.

Jakubowski, M. 1974. Structure of the lateral-line canal system and related bones in the berycoid fish *Hoplostethus mediterraneus* Cuv. et Val. Trachichthyidae, Pisces. Acta Anat. 87: 261–274.

Jielof, R., A. Spoor, and H. de Vries. 1952. The microphonic activity of the lateral line. J. Physiol. (Lond.) 116: 137–157.

Katsuki, Y., and N. Omada. 1973. The lateral-line organs of fish as a chemoreceptor. Pages 389–411 *in* W. Chavin, ed. Responses of fish to environmental changes. Charles C. Thomas, Springfield, Illinois.

Kuiper, J. W. 1967. Frequency characteristics and functional significance of the lateral line organ. Pages 105–121 *in* P. H. Cahn, ed. Lateral line detectors. Indiana University Press, Bloomington.

Merrilees, M. J., and E. J. Crossman. 1973. Surface pits in the family Esocidae. I. Structure and types. J. Morphol. 141: 307–320.

Moore, G. A., and W. E. Burris. 1956. Description of the lateral-line system of the pirate perch, *Aphredoderus sayanus*. Copeia 1956: 18–20.

Munz, H. 1979. Morphology and innervation of the lateral line system in *Sarotherodon niloticus* (L.) (Cichlidae, Teleostei). Zoomorphologie 93:73–86.

Neave, F. 1946. Development of the lateral line organs in salmonids. Trans. R. Soc. Can. 5: 113–118.

Pearson, A. A. 1936. The acoustico-lateral nervous system in fishes. J. Comp. Neurol. 64: 235–273.

Pehrson, T. 1944. The development of latero-sensory canal bones in the skull of *Esox lucius*. Acta Zool. (Stockh.) 25: 135–157.

Petraitis, R. 1966. Fine structure of supporting cells in the lateral-line canal-organ of *Fundulus*. J. Morphol. 118: 367–378.

Rajbanshi, V. K. 1964. Note on the histological study of the lateral line sense organs of *Mystus vittatus*. Curr. Sci. (Bangalore) 16: 492–493.

Reno, H. W., and F. F. Davidson. 1971. Algae Chlorophyta and Chrysophyta in the lateral-line canals of a gizzard shad *Dorosoma cepedianum*. Texas J. Sci. 23: 146–148.

Roberts, B. L., and I. J. Russell. 1972. The activity of lateral-line efferent neurones in stationary and swimming dogfish. J. Exp. Biol. 57: 435–448.

Roberts, B. L., and K. P. Ryan. 1971. The fine structure of the lateral-line sense organ of dogfish. Proc. R. Soc. Lond. B. 179: 157–169.

Sand, A. 1937. The mechanism of the lateral sense organ of fishes. Proc. R. Soc. Lond. B. Biol. Serv. 123B: 472–495.

Sano, Y., K. Hamana, and M. Kawamoto. 1962. Entwicklungsgeschichtliche Untersuchungen am kaudalen neurosekretoreschen System von *Salmo irideus*. Acta Anat. Nippon. 37: 117–125.

Sato, M. 1955. Studies on the pit organs of fishes. I. Histological structure of the large pit organs. Jpn. J. Zool. 11: 443-452.

Sato, M., and N. Katagiri. 1969. Preliminary report on the fine structure of the receptor cells of the small pit organ of the catfish, *Parasilurus asotus*. Jpn. J. Ichthyol. 16: 115-119.

Shelton, P. 1971. The structure and function of the lateral line in larval *Xenopus laevis*. J. Exp. Zool. 178: 211-231.

Sideleva, V. G. 1979. Morphological characteristics of the lateral line system in the eurasian sculpin of the subfamily Cottinae (Cottidae). J. Ichthyol. (Engl. Transl. Vopr. Ikhtiol.) 19: 45–55.

Sutterlin, A. M., and S. Waddy. 1975. Possible role of the posterior lateral line in obstacle entrainment by brook trout (*Salvelinus fontinalis*). J. Fish. Res. Board Can. 32: 2441-2446.

Tester, A. L., and J. I. Kendall. 1968. Cupulae in shark neuromasts: composition, origin, generation. Science 160: 772–774.

Vladykov, V. 1926. Postranni system u celedi Salmonidae. Dil. 1. Topografie a hystologie postranniho systemu u pstruha obecneho (*Trutta fario* L.) [Lateral line system in Salmonidae. Part 1. Topography and histology of lateral system in common trout (*Trutta fario* L.)] Spisy Vydavane Prirodoved. Fak. Karlovy Univ., No. 57: 38 pp. [In Czechoslovakian; Transl. avail. U.S. Natl. Mar. Fish. Serv., Foreign Fish. Transl., Washington, D. C.]

Walker, T. J. 1967. History, histological methods and details of the structure of the lateral line of the walleye surfperch. Pages 13–25 *in* P. H. Cahn, ed. Lateral line detectors. Indiana University Press, Bloomington.

Weber, D. D., and M. H. Schiewe. 1976. Morphology and function of the lateral line of juvenile steelhead trout in relation to gas-bubble disease. J. Fish Biol. 9: 217–233.

Auditory Tissue

Enger, P. S. 1968. Hearing in fish. Pages 4–17 *in* A. V. S. de Reuck and J. Knight, eds. Hearing mechanisms in vertebrates. Churchill, London.

Fay, R. R., and A. N. Popper. 1980. Structure and function in teleost auditory systems. Pages 3–42 *in* A. N. Popper and R. R. Fay, eds. Proceedings Life Science, Comparative studies of hearing in vertebrates. Springer-Verlag, New York.

Lowenstein, O. 1932. Experimentelle Untersuchungen uber den Gleichgewichtssinn der Elritze (*Phoxinus laevis* L.). Z. Vergleich. Physiol. 17: 806–854.

Lowenstein, O. 1936. The equilibrium function of the vertebrate labyrinth. Biol. Rev. Camb. Philos. Soc. 11: 113-145.

Lowenstein, O. 1971. The labyrinth. Pages 207–240 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 5. Academic Press, New York.

Lowenstein, O., M. P. Osborne, and J. Wersall. 1964. Structure and innervation of the sensory epithelia of the labyrinth in the thornback ray (*Raja clavata*). Proc. R. Soc. Lond. B160: 1–12.

Lowenstein, O., M. P. Osborne, and R. A. Thornhill. 1968. The anatomy and ultrastructure of the labyrinth of the lamprey (*Lampetra fluviatilis* L.). Proc. R. Soc. Lond. B170: 113–134.

Manning, F. B. 1924. Hearing in the goldfish in relation to the structure of its ear. J. Exp. Zool. 41: 5–20.

Parker, G. H., and A. P. van Heusen. 1917. The reception of mechanical stimuli by the skin, lateral line organs and ears in fishes, especially in *Ameiurus*. Am. J. Physiol. 44: 463–489.

Popper, A. N. 1981. Comparative scanning electron microscopic investigations of the sensory epithelia in the teleost sacculus and lagena. J. Comp. Neurol. 200: 357–374.

Tavolga, W. N., and J. Wodinsky. 1963. Auditory capacities in fishes. Pure tone thresholds in nine species of marine teleosts. Bull. Am. Mus. Nat. Hist. 126: 177–240.

Pineal Organ

Breder, C. M., and P. Rasquin. 1950. A preliminary report on the role of the pineal organ in the control of pigment cells and light reactions in recent teleost fishes. Science 111: 10–12.

Breucker, H., and E. Horstmann. 1965. Elektronenmikroskopische Untersuchungen am Pinealorgan der Regenbogenforelle (*Salmo irideus*). Progr. Brain. Res. 10: 259–269.

de Vlaming, V. L. 1975. Effects of pinealectomy on gonadal activity in the cyprinid teleost, *Notemigonus crysoleucas*. Gen. Comp. Endocrinol. 26: 36–49.

Dodt, E. 1963. Photosensitivity of the pineal organ in the teleost, *Salmo irideus* (Gibbons). Experientia 19: 642–643.

Falcon, J. 1979. The pineal organ of the pike, *Esox lucius* L. I. A light and electron microscopic study. Ann. Biol. Anim. Biochim. Biophys. 19: 445–465.

Falcon, J., and H. Meissl. 1981. The photosensory function of the pineal organ of the pike (*Esox lucius* L.). Correlation between structure and function. J. Comp. Physiol. 144 Part A: 127–138.

Fenwick, J. C. 1970. The pineal organ. Pages 91–108 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 4. Academic Press, New York.

Hafeez, M. A. 1971. Light microscopic studies on the pineal organ in teleost fishes with special regard to its function. J. Morphol. 134: 281–314.

Hafeez, M. A., and P. Ford. 1967. Histology and histochemistry of the pineal organ in the sockeye salmon, *Onchorhynchus nerka* Walbaum. Can. J. Zool. 45: 117–126.

Hartwig, H. G. 1973. Scanning electron microscopic observations of pineal photoreceptor cells in the trout, *Salmo gairdneri* (Teleostei). Z. Zellforsch. Mikrosk. Anat. 138: 585–589.

Hoar, W. S. 1955. Phototactic and pigmentary responses of sockeye salmon smolts following injury to the pineal organ. J. Fish. Res. Board Can. 12: 178–185.

Jansen, W. F., H. von Loveren, R. A. Woutersen, and R. A. de Weger. 1976. Enzyme cytochemistry of the saccus dorsalis of the rainbow trout *Salmo gairdneri* Richardson. Histochemistry 43: 293–306.

Korf, H. W. 1974. Acetylcholinesterase-positive neurons in the pineal and parapineal organs of the rainbow trout, *Salmo gairdneri* (with special reference to pineal tract). Cell Tissue Res. 155: 475–489.

Kelly, D. E. 1962. Pineal organs: Photoreception, secretion and development. Am. Sci. 50: 597–625.

McNulty, J. A., and B. G. Nafpaktitis. 1976. The structure and development of the pineal complex in the lanternfish *Triphoturus mexicanus* (family Myctophidae). J. Morphol. 150: 579–606.

Murphy, R. C. 1971. The structure of the pineal organ of the bluefin tuna, *Thunnus thynnus*. J. Morphol. 133: 1–15.

Oguri, M., and Y. Omura. 1973. Ultrastructure and functional significance of the pineal organ of teleost. Pages 412–434 in W. Chavin, ed. Responses of fish to environmental changes. Charles C. Thomas, Springfield, Illinois.

Omura, Y. 1975. Influence of light and darkness on the ultrastructure of the pineal organ in the blind cavefish, *Astyanax mexicanus*. Cell Tissue Res. 160: 99–112.

Omura, Y. 1979. Light and electron microscopic studies on the pineal tract of rainbow trout, *Salmo gairdneri*. Rev. Can. Biol. 38: 105–118.

Omura, Y., and M. Oguri. 1969. Histological studies on the pineal organ of 15 species of teleosts. Bull. Jpn. Soc. Sci. Fish. 35: 991–1000.

Omura, Y., J. Kitoh, and M. Oguri. 1969. The photoreceptor cell of the pineal organ of ayu, *Plecoglossus altivelis*. Bull. Jpn. Soc. Sci. Fish. 35: 1067–1071.

Rasquin, P. 1958. Studies in the control of pigment cells and light responses in recent teleost fishes. 1. Morphology of the pineal region. 2. Reactions of the pigmentary system to hormonal stimulation. Bull. Am. Mus. Nat. Hist. 115: 7–68.

Rivas, L. R. 1953. The pineal apparatus of tunas and related scombrid fishes as a possible light receptor controlling phototactic movements. Bull. Mar. Sci. Gulf Caribb. 3: 168–180.

Rudeberg, C. 1969. Structure of the parapineal organ of the adult rainbow trout, *Salmo gairdneri* Richardson. Z. Zellforsch. Mikrosk. Anat. 93: 282–304.

Tabata, M., T. Tamura, and H. Niwa. 1975. Origin of the slow potential in the pineal organ of the rainbow trout. Vision Res. 15: 737–740.

Takahashi, H. 1969. Light and electron microscopic studies on the pineal organ of the goldfish, *Carassius auratus* L. Bull. Fac. Fish. Hokkaido Univ. 20: 143–157.

Veen, Th. van, P. Ekstrom, B. Borg, and M. Moller. 1980. The pineal complex of the three-spined stickleback, *Gasterosteus aculeatus* L. A light-electron microscopic and fluorescense histochemical investigation. Cell Tissue Res. 209: 11–28.

Rodlet Cells

Bannister, L. H. 1965*a*. The structure of *Rhabdospora thelchani*, a parasitic protozoan of uncertain affinities. Excerpta Med. Int. Congr. Ser. 91: 180.

Bannister, L. H. 1965*b*. The fine structure of the olfactory surface of teleostean fishes. Q. J. Microsc. Sci. 106: 333–342.

Bannister, L. H. 1966. Is *Rhabdospora thelchani* (Laguesse) a sporozoan parasite or a tissue cell of lower vertebrates? Parasitology 56: 633–638.

Barber, D. L., and J. E. M. Westerman. 1975. "Rodlet cells" in *Catostomus commersonii* (Teleostei: Pisces): secretory or parasite? Experientia 31: 924–925.

Barber, D. L., J. E. M. Westerman, and D. N. Jensen. 1979. New observations on the rodlet cell (*Rhabdospora thelchani*) in the white sucker *Catostomus commersoni* (Lacepede): LM and EM studies. J. Fish Biol. 14: 277–284.

Desser, S. S., and R. Lester. 1975. An ultrastructural study of the enigmatic "rodlet cells" in the white sucker, *Catostomus commersoni* (Lacepede) (Pisces: Catostomidae). Can. J. Zool. 53: 1483–1494.

Flood, M. T., R. F. Nigrelli, and J. F. Gennaro, Jr. 1975. Some aspects of the ultrastructure of the "Stabchendrusenzellen," a peculiar cell associated with the endothelium of the bulbus arteriosus and with other fish tissues. J. Fish Biol. 7: 129–138.

Hirji, K. N., and W. A. Courtney. 1979. "Pear-shaped" cells in the digestive tract of the perch *Perca fluviatilis* (L.). J. Fish Biol. 15: 629–632.

Iwai, T. 1968. Studies on the pear-shaped cell (rodlet cell) in the epithelium of the digestive tract of fishes. Bull. Jpn. Soc. Sci. Fish. 34: 133–137. [In Japanese]

Kimura, N. 1973. Fine structure of pear-shaped cells and "vesicle-rich cells" in pyloric caeca of rainbow trout. Jpn. J. Ichthyol. 20: 94–106.

Leino, R. L. 1972. Ultrastructure and development of rodlet cells in gill and intestine of walleyed pike *Stizostedion vitreum*. Proc. Electron Microsc. Soc. Am. 30: 264–265.

Leino, R. L. 1974. Ultrastructure of immature, developing and secretory rodlet cells in fish. Cell Tissue Res. 155: 367–381.

Leino, R. L. 1979. Aspects of the fine structure, cytochemistry and distribution of teleost rodlet cells. Ph.D. Thesis. Union Graduate School, Cincinnati. 166 pp.

Mattey, D. L., M. Morgen, and D. E. Wright. 1979. Distribution of rodlet cells in the gills and pseudobranch of the bass, *Dicentrachus labrax* (L.). J. Fish Biol. 15: 363–370.

Mayberry, L. F., A. A. Marchiondo, J. E. Ubelaker, and D. Kazic. 1979. *Rhabdospora thelohani* Laguesse, 1895 (Apicomplexa): new host and geographic records with taxonomic considerations. J. Protozool. 26: 168–178.

Modin, J. C. 1981. *Microsporidium rhabdophilia* n. sp. from rodlet cells of salmonid fishes. J. Fish Dis. 4: 203–211.

Morrison, C. M., and P. H. Odense. 1978. Distribution and morphology of the rodlet cell in fish. J. Fish. Res. Board Can. 35: 101–116.

Mourier, J. P. 1970. Structure fine de *Rhabdospora thelohani* Henneguy, protiste parasite de *Gasterosteus aculeatus*. Z. Parasitenkd. 34: 198–206.

Thelohan, P. 1892. Sur des sporozoares indetermines parasites des poissons. J. Anat. Physiol. (Paris) 28: 163–171.

Plate 41. Optic Tissue

Fig. 1. Median section through the eye of 3-month-old rainbow trout. × 40.

a. Retina (see Fig. 3)
b. Optic nerve (optic disk)
c. Lens
d. Iris
e. Cornea
f. Corneal epithelium
g. Choroid gland (see Fig. 4)

Fig. 2. Detail of cornea. × 250.

a. Corneal epithelium
b. Bowman's membrane
c. Cornea
d. Descemet's membrane
e. Descemet's endothelium

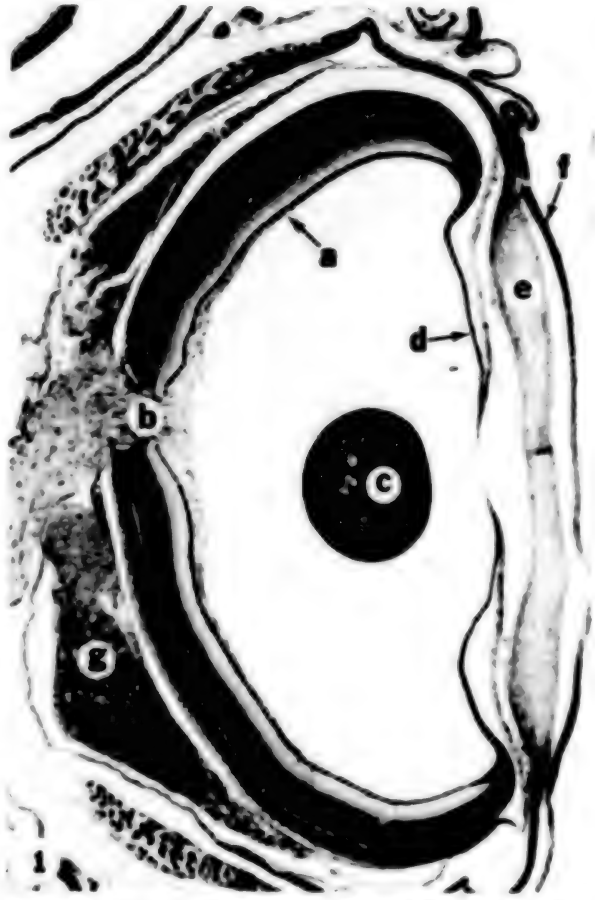
Fig. 3. Detail of retina (Fig. 1). × 250.

a. Capillary layer of the choroid
b. Pigment epithelium (the capillary layer has separated from the pigment epithelium at Bruck's membrane, at arrow).
c. Layer of rods and cones. External limiting membrane, arrow
d. Outer nuclear layer of rods and cones
e. Outer plexiform layer
f. Inner nuclear layer
g. Inner plexiform layer
h. Ganglion cell layer
i. Nerve fiber layer

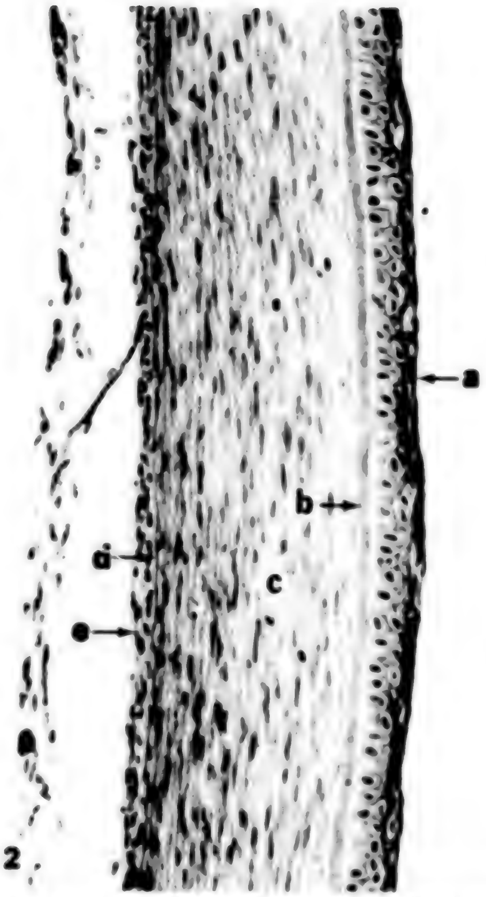
Fig. 4. Detail of the choroid gland. × 530.

a. Afferent capillary
b. Efferent capillary

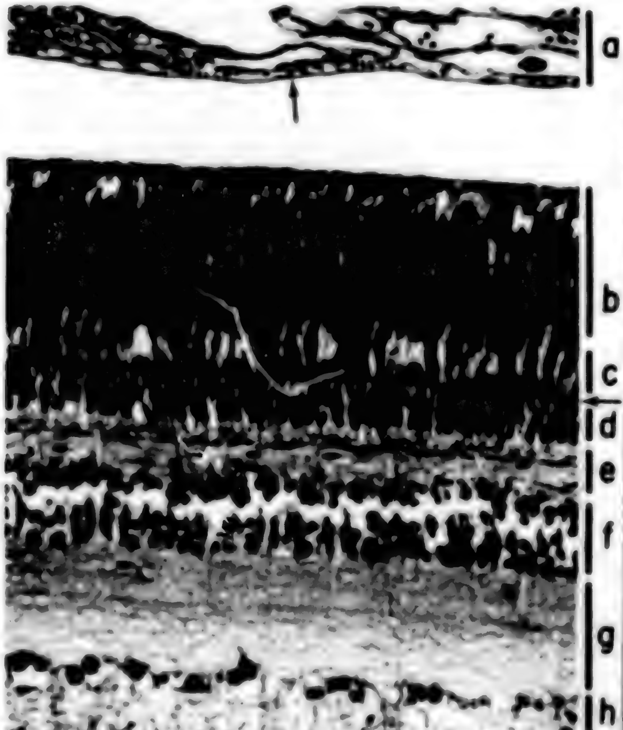
Fig. 5. Eye lens fibers of a yearling rainbow trout. × 5000. Note the interdigitation of marginal protrusions and the numerous perforations in the smooth fiber surface.



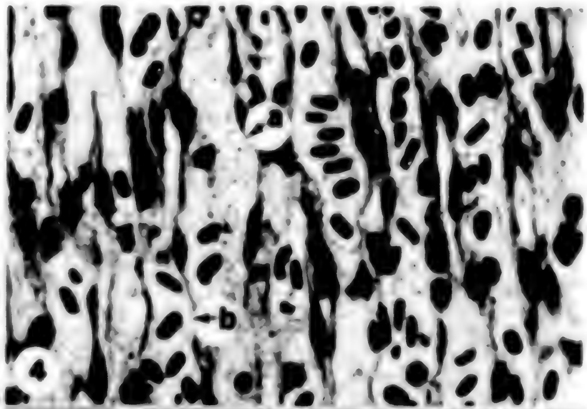
1



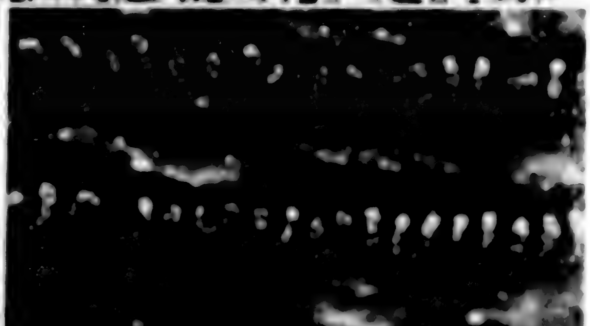
2



3



4



5

Plate 42. Retina.

Rainbow trout 3 months old. Masson's trichrome stain. × 625.

b. Pigment epithelium
c. Layer of rods and cones
d. Outer nuclear layer
e. Outer plexiform layer
f. Inner nuclear layer
g. Inner plexiform layer
h. Ganglion cell layer
i. Nerve fiber layer

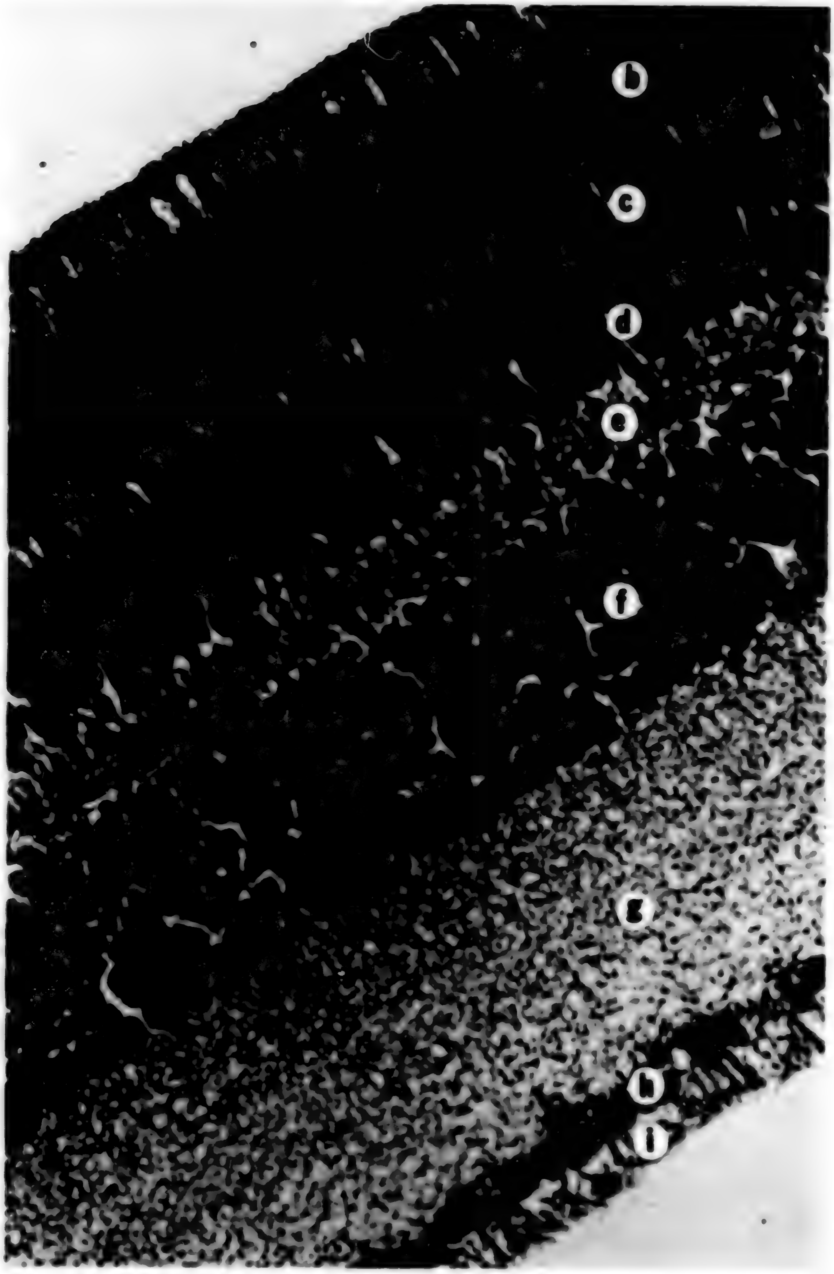

b
c
d
e
f
g
h
i

Plate 43. Olfactory Tissue

Fig. 1. Section of the olfactory capsule of a 9-month-old rainbow trout. × 40.

- a. Lamella with connective tissue core
- b. Ciliated epithelium

Fig. 2. Cross section of the terminus of the olfactory sac. × 250.

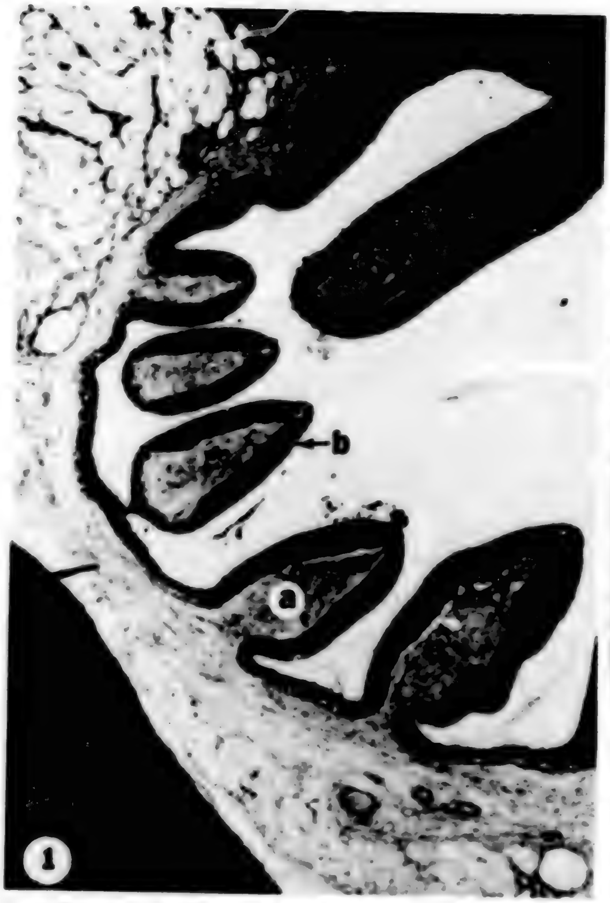
- a. Supporting connective tissue
- b. Ciliated epithelium

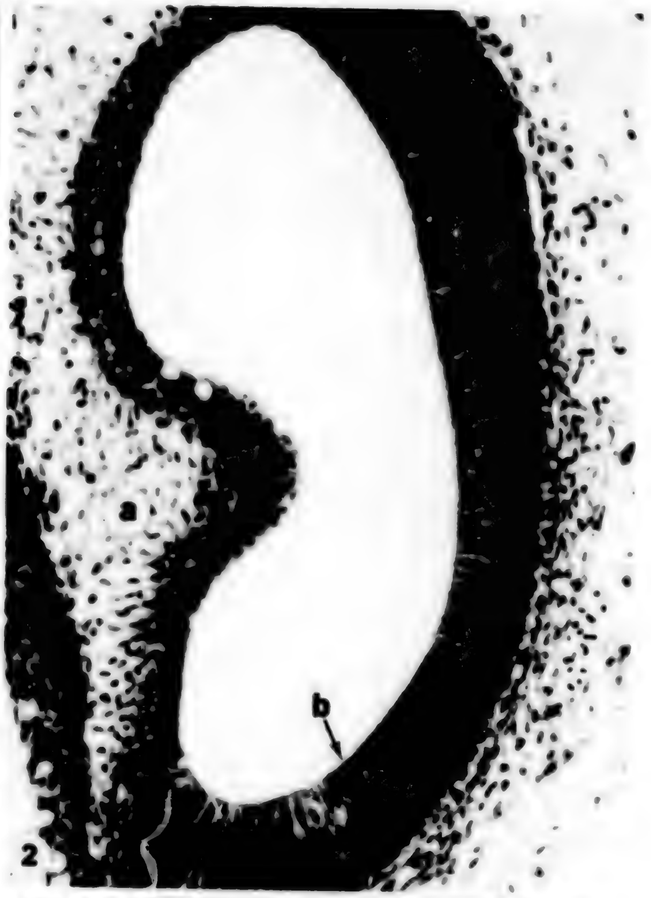
Fig. 3. Section of the nasal pouch, contrasting the two layers of epithelium. × 250.

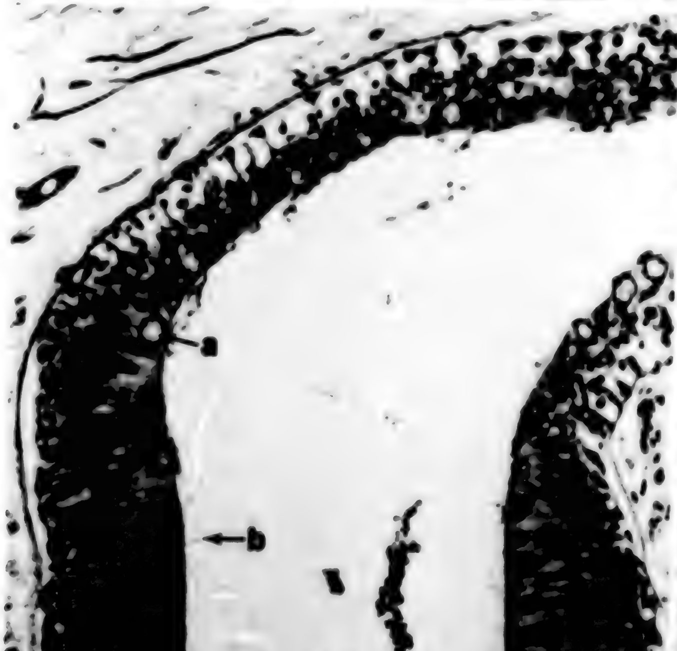
- a. Goblet cell
- b. Cilia of ciliated epithelium

Fig. 4. Detail of sensory epithelium. Note that the layer of sensory cells has lifted from the basement membrane and supporting connective tissue. × 560.

- a. Nucleus of an epithelial cell
- b. Wandering lymphocyte
- c. Cilia of epithelial cell
- d. Columnar epithelial cell
- e. Mucous (or goblet) cell
- f. Basal cell


b
a
1


a
b
2


a
b
3

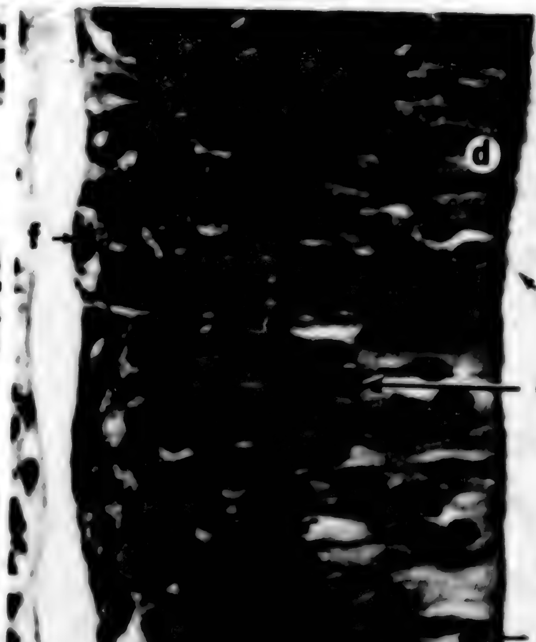

d
f
c
a
b
e
4

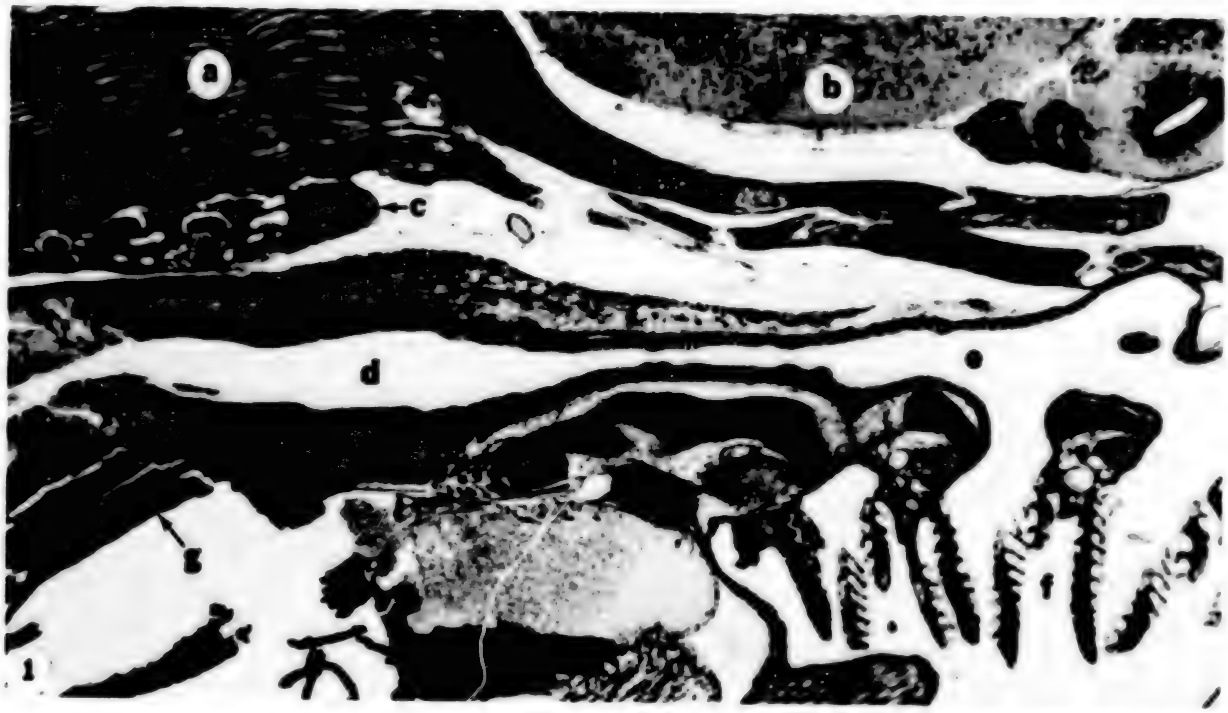
Plate 44. Gustatory Tissue

Fig. 1. Sagittal section through the pharyngeal region of the digestive tract of 1-month-old rainbow trout. × 60.

a. Musculature
b. Brain
c. Kidney
d. Esophageal region
e. Pharyngeal region
f. Gills
g. Remnant of yolk

Fig. 2. Detail of pharyngeal region (Fig. 1). × 300.

a. Muscularis (cross section)
b. Pharyngeal-esophageal region
c. Taste bud
d. Lamina propria
e. Submucosa
f. Basibranchium


a
b
c
d
e
g
f
1

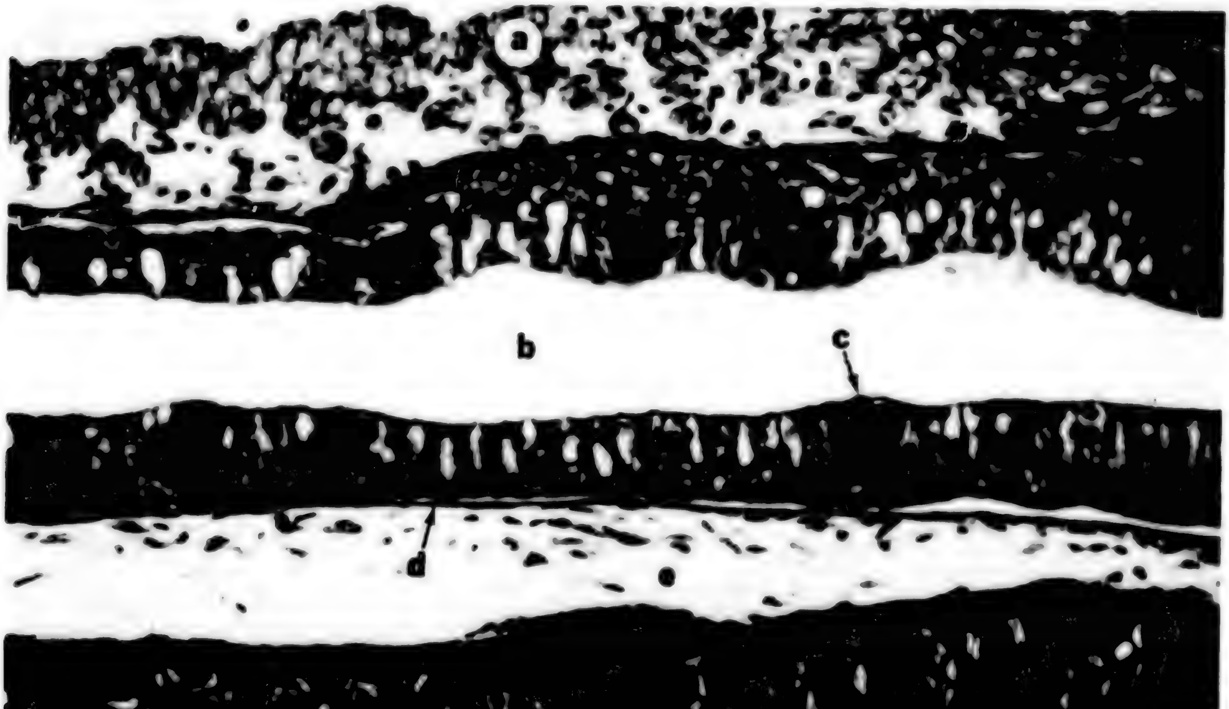

a
b
c
d
e
f
2

Plate 45. Tactile Organs

Fig. 1. Sensory organ located near the eye of 3-month-old rainbow trout. × 725.

a. Sensory papilla. Note the sensory filaments projecting from the sensory cells.
b. Mucous cell
c. Melanophore
d. Dermis
e. Nerve fibers extending into the papilla

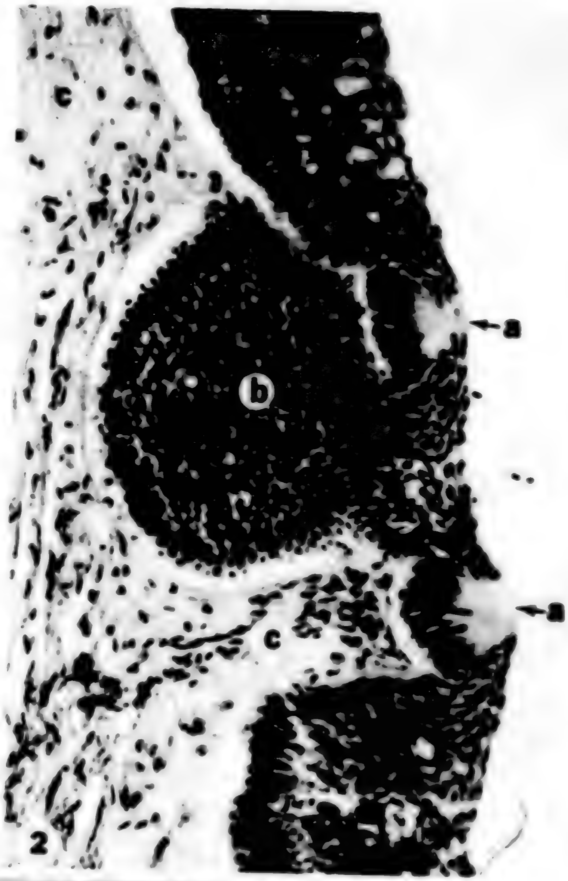
Fig. 2. Cutaneous sense organs in the skin of adult brook trout. × 250.

a. Sensory papilla
b. Invagination of the epidermis
c. Papilla of the dermal layer (stratum vasculare)

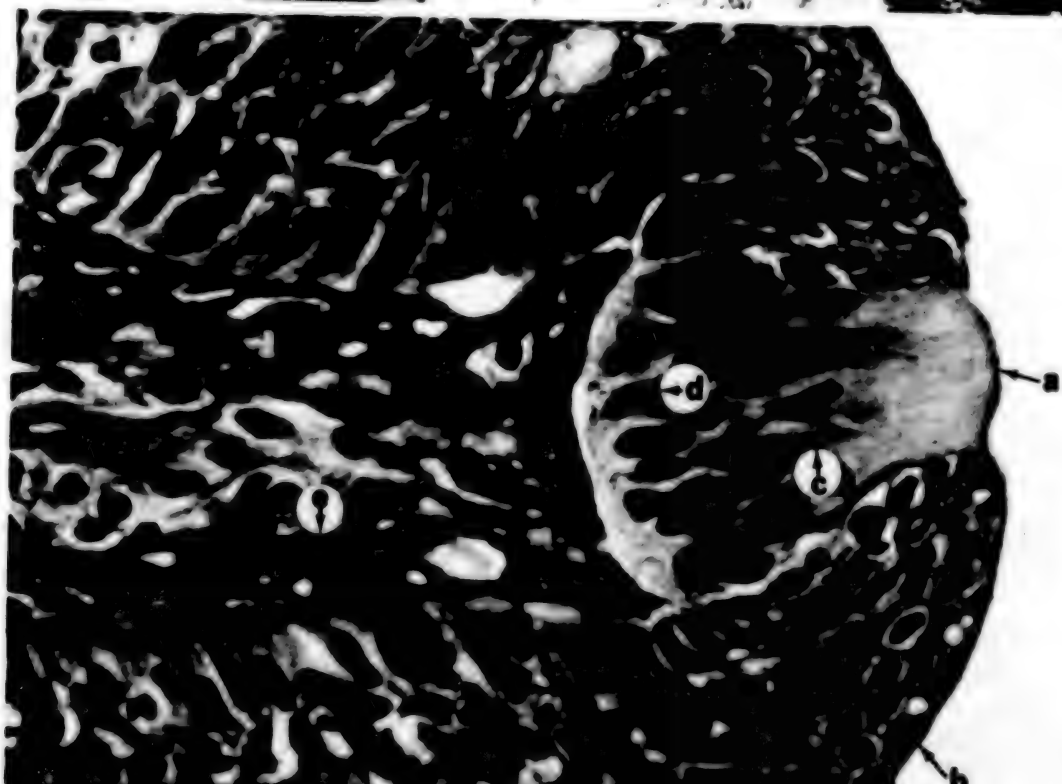
Fig. 3. Taste bud from the esophageal region of 3-month-old rainbow trout. × 725.

a. Sensory papilla within the sensory pit
b. Stratified squamous epithelium
c. Nuclei of the neuro-epithelial cells
d. Nuclei of supporting cells
e. Nerve fibers of sensory cells

1



2



3

Plate 46. Lateral Line Tissue

Fig. 1. Cross section of the lateral line tissues of a 4-month-old rainbow trout. × 40.

- a. Lateral line canals of two consecutive scales (within box)
- b. Dense connective tissue of the stratum compactum
- c. Lymph vessel
- d. Lateral line nerve
- e. Lateral musculature in cross section
- f. Blood vessel
- g. Intermuscular adipose tissue

Fig. 2. Detail of lateral line canals (boxed area of Fig. 1). × 250.

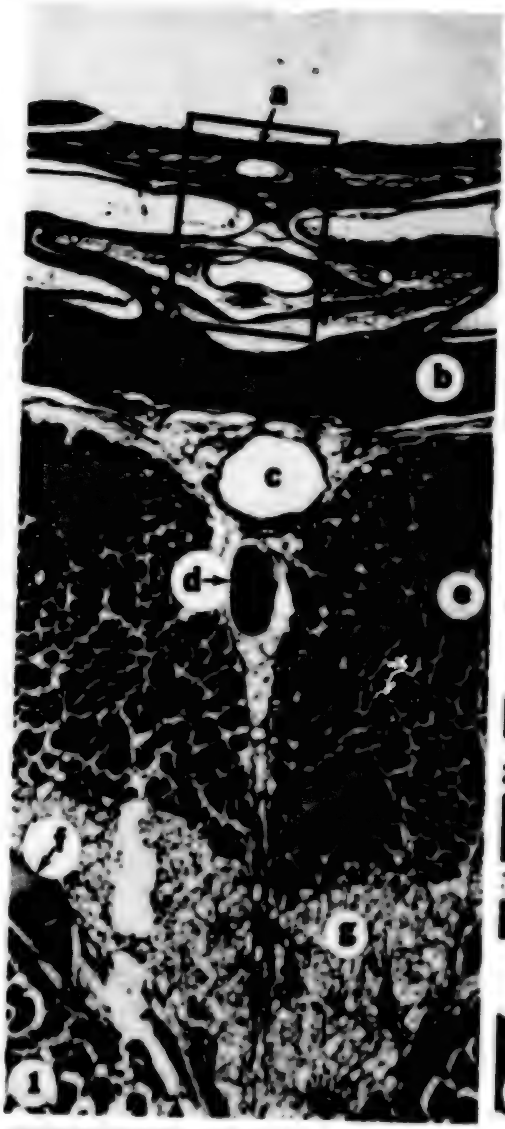
- a. Goblet cell in epidermis
- b. Epithelium of lateral line canal
- c. Scale
- d. Filamentous processes of the sensory cells
- e. Sensory cells
- f. Stratum spongiosum of the dermis

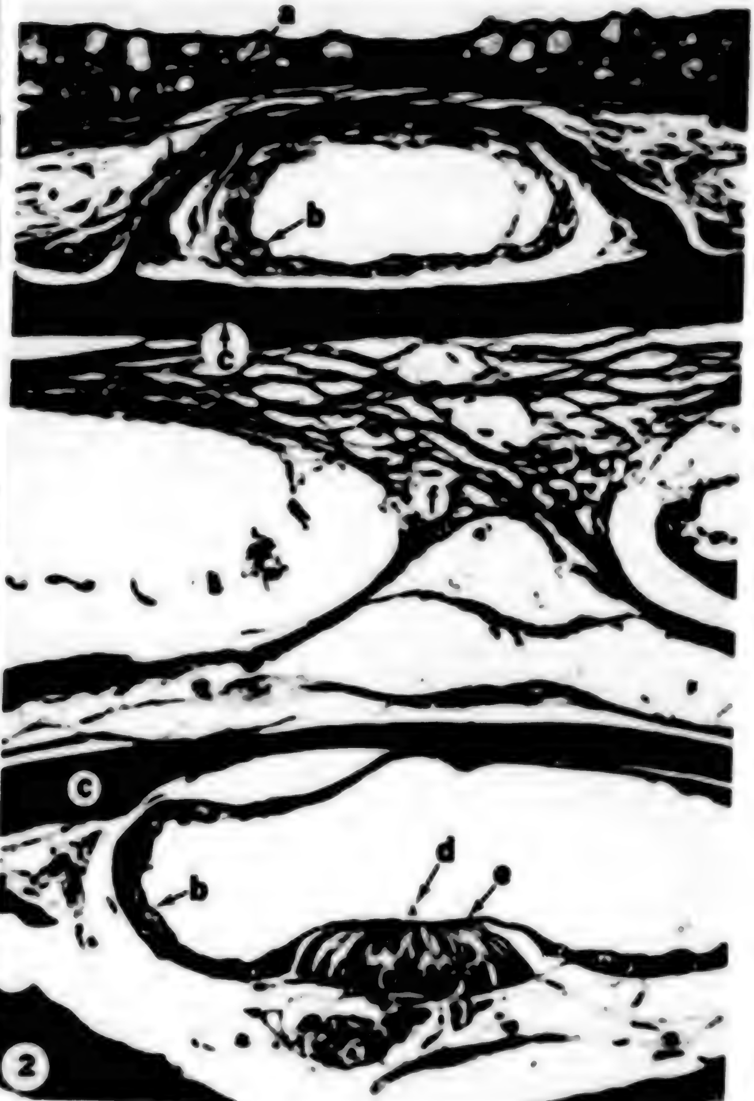
Fig. 3. Longitudinal section of the head of 4-month-old rainbow trout, showing a sensory pore of the hyomandibular canal lying above the posterior arm of the horizontal semicircular canal. × 40.

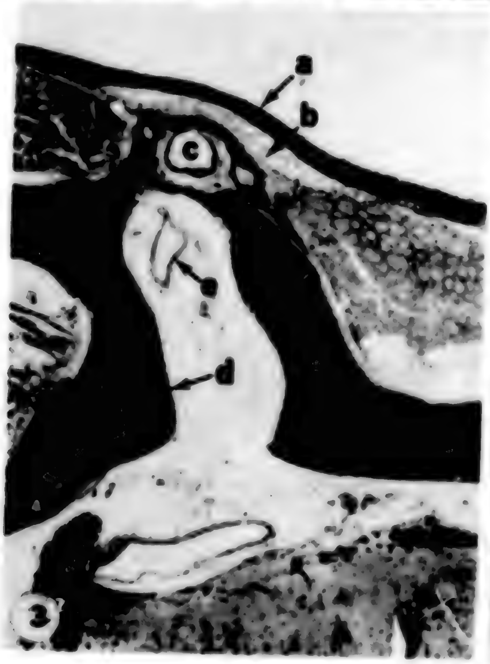
- a. Skin
- b. Loose connective tissue
- c. Sensory pore
- d. Cranial cartilage
- e. Semicircular canal

Fig. 4. Details of sensory pore (Fig. 3c) sectioned at a different level. × 250.

- a. Pyriform receptor cells
- b. Portion of the cupula
- c. Cross section of the bony hyomandibular canal


a
b
c
d
e
f
g
1


a
b
c
f
c
b
d
e
2


a
b
c
e
d
3

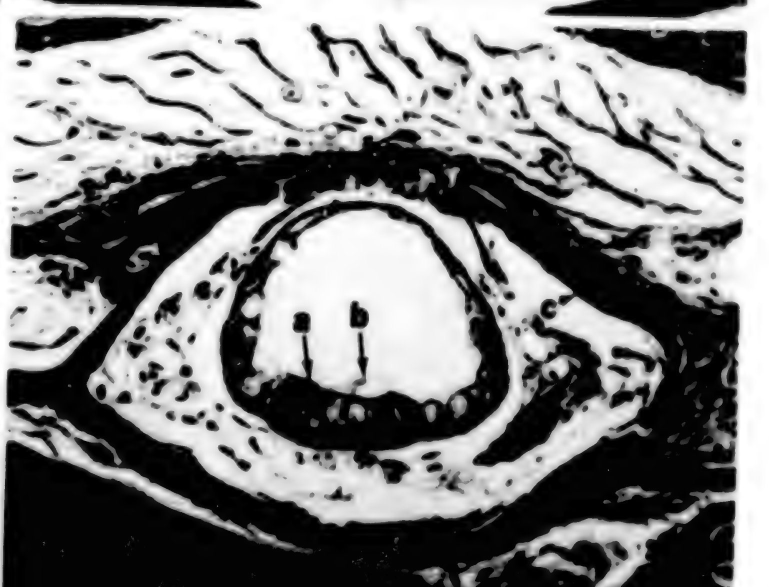

c
a
b
c
4

Plate 47. Lateral Line Tissue

Cross section of 6-month-old rainbow trout. Hematoxylin and eosin stain. × 240.

a. Epidermis
b. Scale
c. Cupula
d. Pyriform receptor cells
e. Dermis
f. Lymph vessel

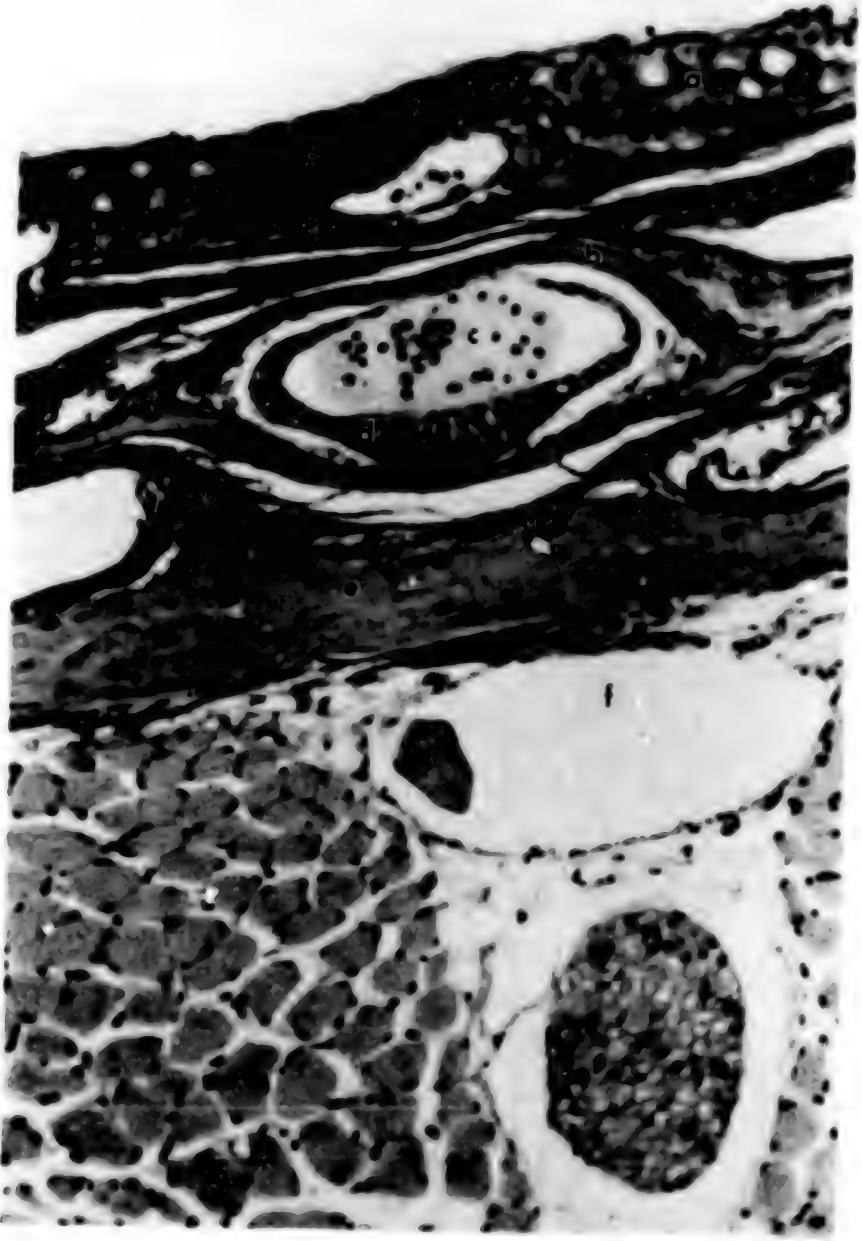

a
b
c
d
f

Plate 48. Auditory Tissue

Fig. 1. Horizontal section through the head of 1-month-old rainbow trout, showing the location of the semicircular canals. Note that the membranous lining of the canals has drawn away from the surrounding cartilage. × 40.

a. Thymus gland lying posterior to the cranium
b. Cartilage of the cranium
c. Metencephalon (cerebellum)
d. Mesencephalon (optic lobe)
e. Portion of the posterior vertical semicircular canal
f. Portion of the horizontal semicircular canal
g. Portion of the anterior vertical semicircular canal
h. Pore of the cephalic lateral line system

Fig. 2. Sagittal section through the head (laterally) of 1-month-old rainbow trout. × 40.

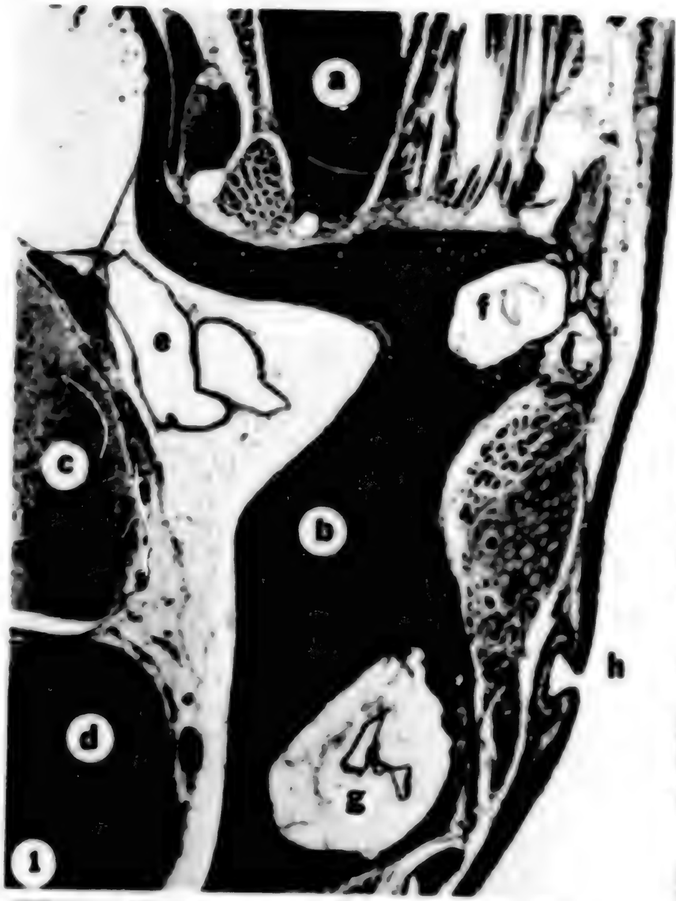
a. Metencephalon (cerebellum)
b. Mesencephalon (optic lobe)
c. Receptor cells
d. Sacculus with sagitta removed

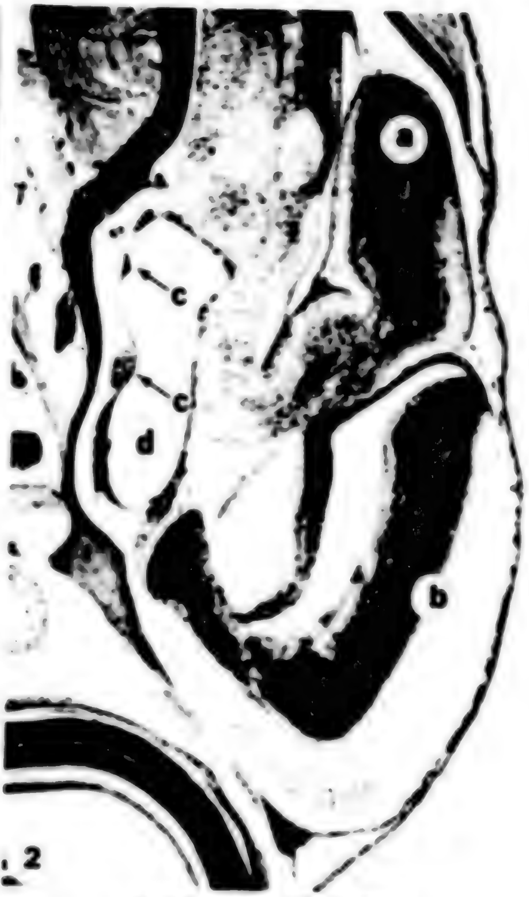
Fig. 3. Longitudinal section through the sacculus and the sagitta of 1-month-old rainbow trout. × 250.

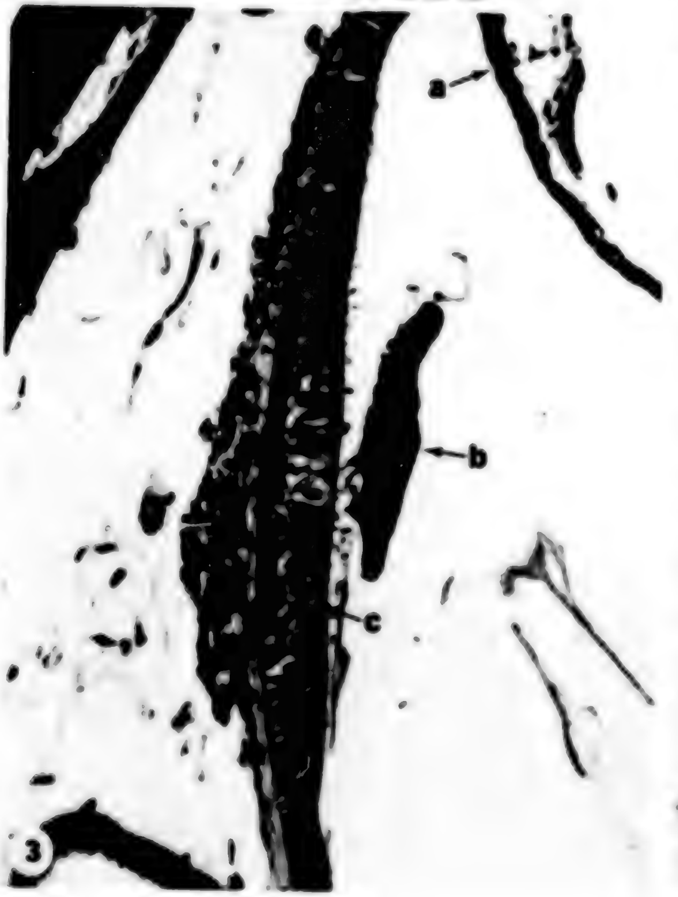
a. Epithelium of the sacculus
b. Sagitta (otolith)
c. Macula

Fig. 4. Detail of the macula of the sacculus. × 560.

a. Sustentacular cell
b. Hair cell nuclei
c. Sensory hairs (filaments)


a
e
f
c
b
h
d
g
1


a
c
c
d
b
2


a
b
c
3

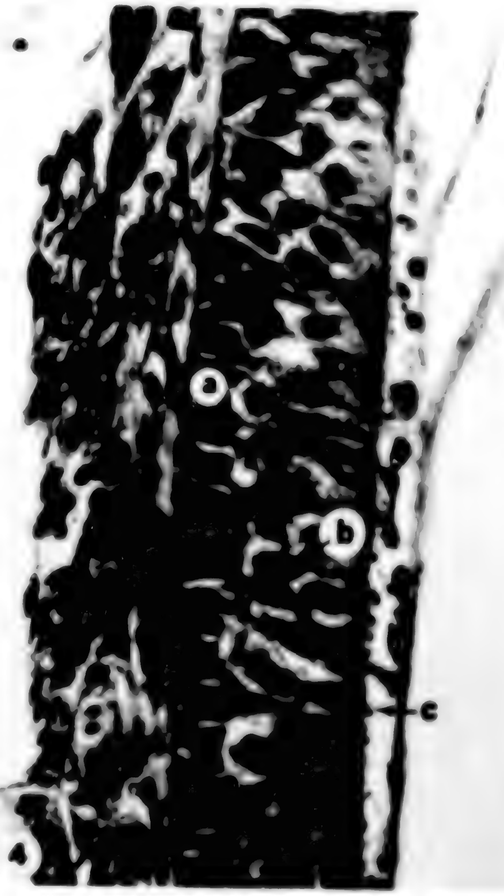

a
b
c
4

Plate 49. Pineal Organ

Fig. 1. Sagittal section of the head of 3-month-old rainbow trout. × 100.

- a. Skin
- b. Connective tissue
- c. Cartilage of cranial roof
- d. Pineal end-vesicle
- e. Telencephalon (forebrain)
- f. Mesencephalon (optic lobe)
- g. Saccus dorsalis

Fig. 2. Pineal end-vesicle and a portion of the saccus dorsalis (Fig. 1d and 1g; × 500)

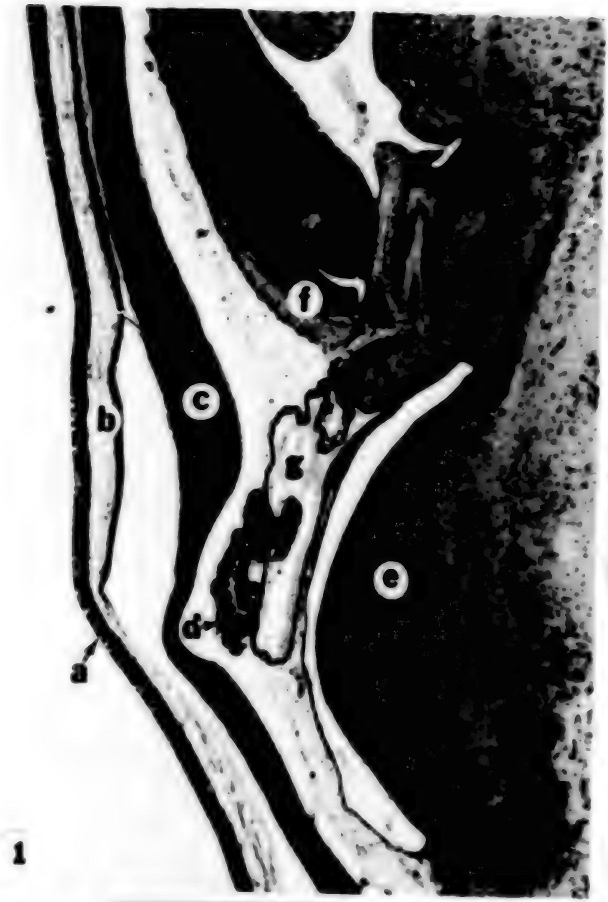
- a. Blood vessel
- b. Sensory cells lining the epithelium of the end-vesicle
- c. Sensory cell axon
- d. Epithelial lining of the saccus dorsalis
- e. Lumen of saccus dorsalis

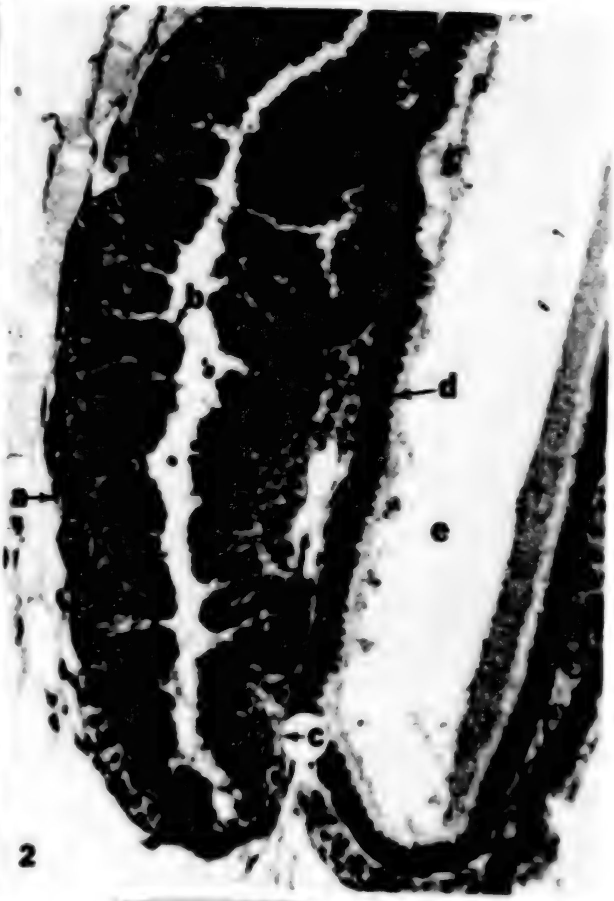
Fig. 3. Section through lateral portion of pineal end-vesicle, showing many deeply staining sensory cell nuclei. × 500.

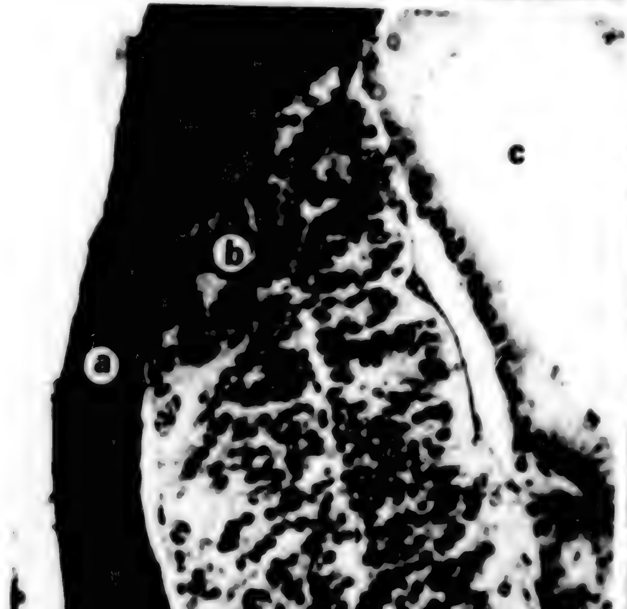
- a. Cranial roof
- b. Pineal end-vesicle
- c. Lumen of saccus dorsalis

Fig. 4. Section of the pineal end-vesicle, showing details of the sensory cells. × 500.

- a. Sensory cells
- b. Ciliary processes of the sensory cells
- c. Supporting cells
- d. Nerve fibers
- e. Lumen of end-vesicle


f
c
b
g
e
d
a
1


b
d
a
e
c
2


c
b
a
3

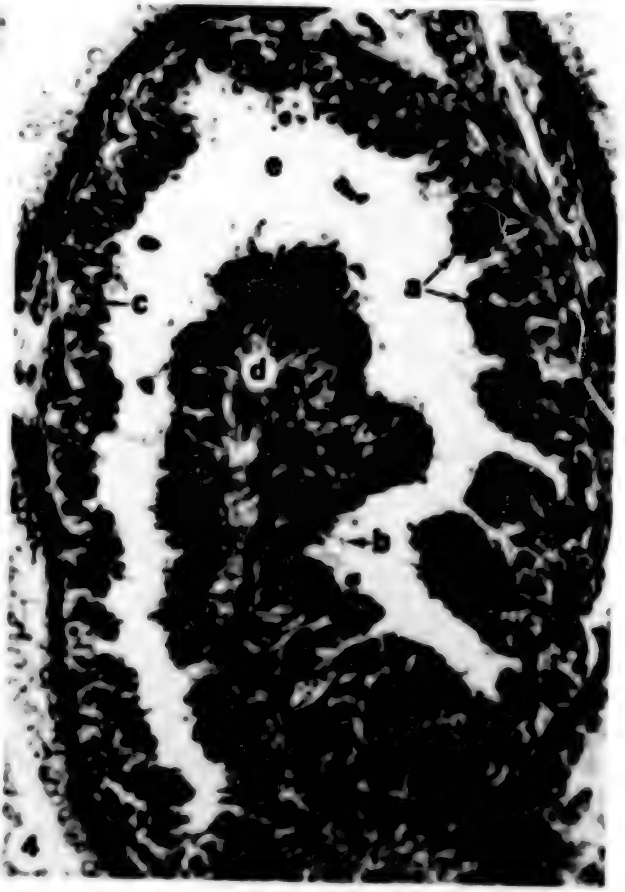

e
a
c
d
b
4

Plate 50. Rodlet Cells (Masson's trichrome stain)

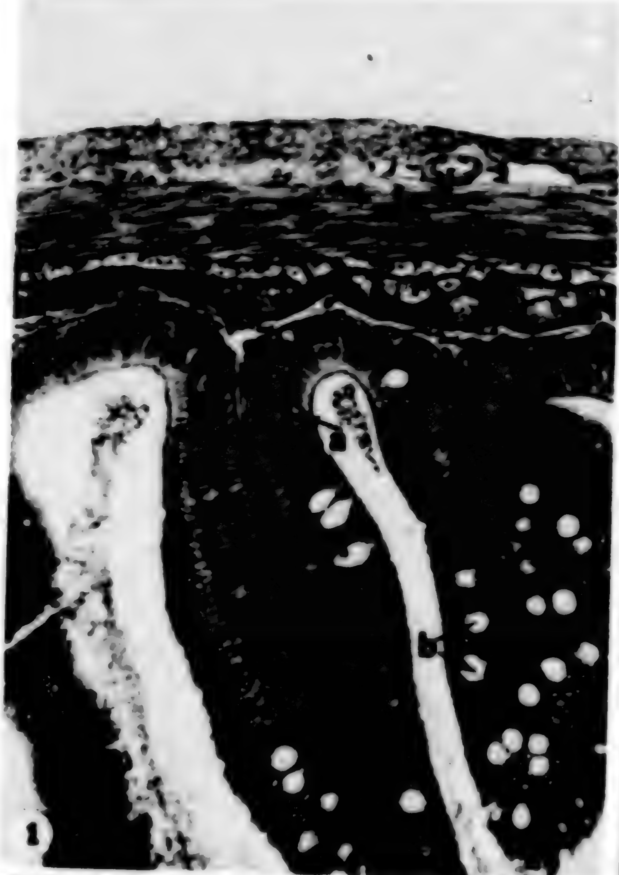
Fig. 1. Cross section of salmonid intestine. × 200.

a. Rodlet cell
b. Mucous cells

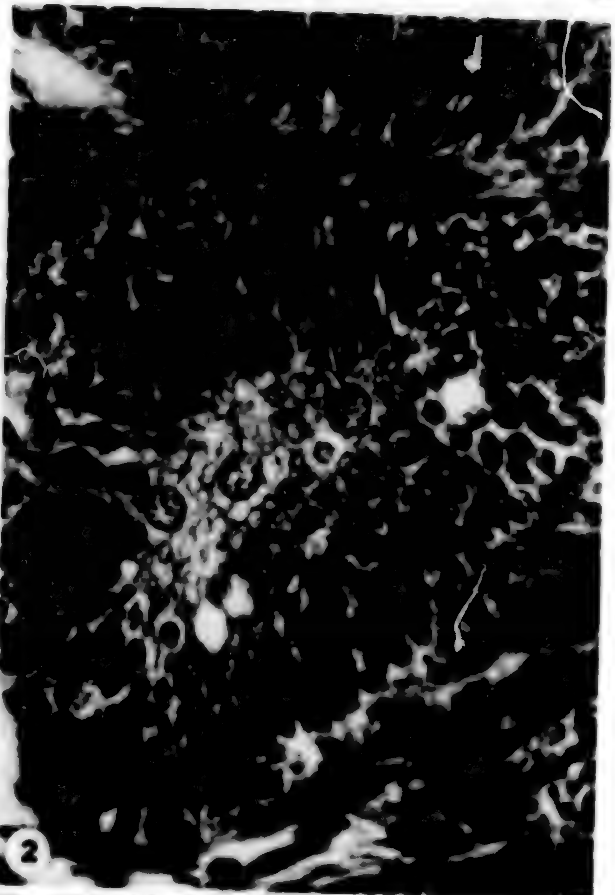
Fig. 2. Three rodlet cells (arrows) viewed in cross section. The characteristic rods within these cells appear as lightly stained spots. × 500.

Fig. 3. Eight rodlet cells can be seen in this section of intestinal mucosa. The uppermost arrow points to a cell in longitudinal profile and the lower two arrows show cells in cross section. × 500.

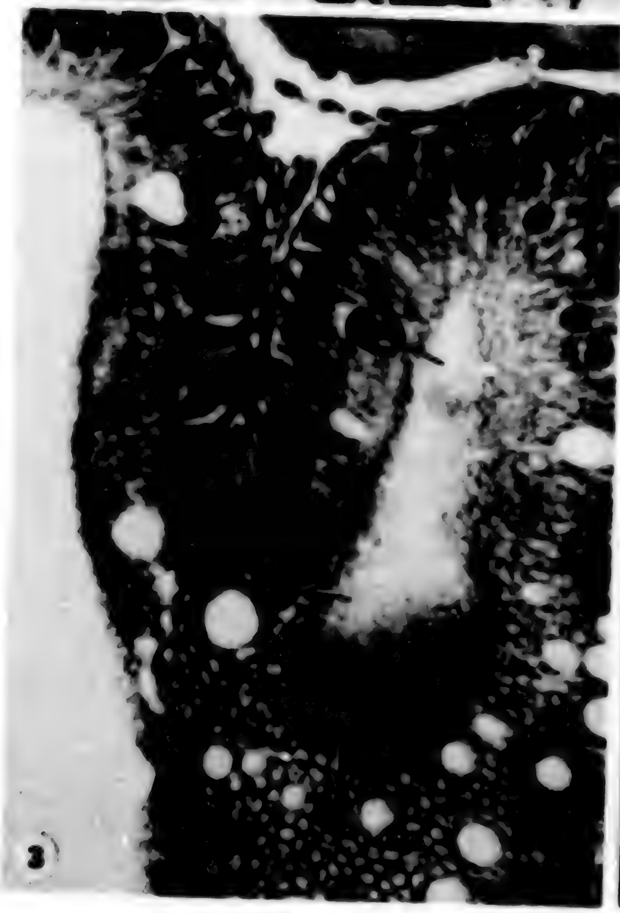
Fig. 4. Five rodlet cells (arrows) in section of intestinal mucosa. The single, saucer-shaped nucleus can be seen in three of the cells. × 500.



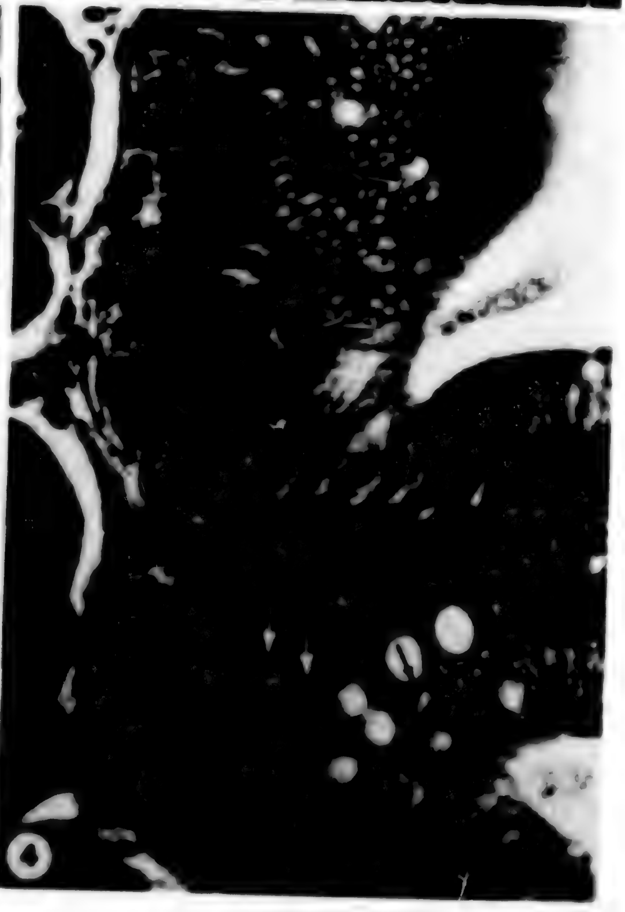
1



2



3



4

Blank Page

Chapter XII

Reproductive System

Testis

A considerable number of descriptive works have been published on the trout testis (Jores 1940; Robertson 1958; Henderson 1962; Oota et al. 1965; Takashima et al. 1980). Weisel (1943) found in a comparative study that the testes of immature and mature sockeye salmon (*Oncorhynchus nerka*) and rainbow trout were similar. There has been some confusion in the past about the gross morphology of trout gonads, particularly the genital ducts and their openings. Henderson (1962) showed that the reproductive and urinary systems are completely separate. In both male and female trout, the urinary duct lies immediately posterior to the genital duct and opens through a separate orifice.

Henderson (1962) called cells in the earliest stage of spermatogenesis the primordial germ cells. Some of these cells divide to form primary spermatogonia and others remain quiescent. The developing spermatogonia divide to form cysts of spermatocytes. Henderson's observations on the brook trout suggested that the germ cells for each succeeding generation came from the primordial germ cells that remained quiescent along the border of the lobule.

A longitudinal section of the testis of a 14-month-old rainbow trout stained with hematoxylin and eosin shows the stroma of connective tissue and the associated blood vessels to be well differentiated (Plate 51, Figs. 1 and 2). The lobule sections appear to vary in size and shape, but this variation is due to the plane of sectioning. Each lobule is packed with spherical spermatogonia of various diameters. Numerous mitotic figures are evident (Plate 51, Fig. 2).

A cross section of the testis of a 19-month-old rainbow trout shows extensive changes in the tissues (Plate 51, Figs. 3 and 4). The lobules are much enlarged and the septa of connective tissue correspondingly stretched into relatively thin "membranes." The lobule walls are divided into cysts, each cyst containing spermatogonia in different stages of development. Most cysts contain primary and secondary spermatocytes and a few contain spermatids nearly ready to be discharged into the lumen of the lobule.

In addition to the tissues of the testis already mentioned, a sheath of connective tissue surrounds the organ and suspends it from the abdominal wall. This suspensory tissue was termed the mesorchium by Henderson (1962), who pointed out that it arises from the peritoneum covering the swim bladder. Underlying this peritoneal sheath is the tunica albuginea, which is composed of fibrous tissue and muscle fibers.

Ovary

Much less research has been done on the ovarian tissues of salmonids than on the testicular tissues. Insofar as we know, only Yamamoto et al. (1965) reported specifically on the maturation of the rainbow trout ovary. However, there are many studies on other species (Chouinard 1963; Hurley and Fisher 1966; Beams and Kessel 1973), and in the ovaries, as in the testes, there are apparently few differences between salmonids and other species of fish.

Fish ovaries are located bilaterally along the sides of the abdominal cavity and are supported in the cavity by the mesovarian mesentery. The lamellae of the ovary are similar to the lobules of the testis. Both of these subdivisions of the gonads permit adequate blood supplies and facilitate escape of sperm and ova. The blood vessels surrounding the lamellae and the lobules are supported by septa of connective tissue. In describing the reproductive cycle of a goby (*Gillichthys*), de Vlaming (1972) observed that internally the ovaries are made up of many branching connective tissue septa. The lamellae projecting into the lumen of the ovary are covered by germinal epithelium. Oogonia, which are periodically generated by the germinal epithelium, produce oocytes. As the oocytes mature, they are released into the lumen of the ovary, covered by a thin sheath of connective tissue. Blood vessels develop in this theca to supply the follicle.

In the maturation of the oocytes, the oogonia are referred to as primary oocytes and secondary oocytes (Plate 52). As the entrance of yolk granules into the cytoplasm (vitellogenesis) proceeds, the oocytes enlarge, the follicular epithelium thickens, and yolk vesicles fill the ooplasm. In essential features, the ovarian maturation of the trout is the same as that of the goby, as described by de Vlaming (1972): "With continued oocyte growth the ooplasm becomes impregnated with yolk globules which are larger than the yolk vesicles, and which stain with hematoxylin. Toward the end of the growth phase, several other morphological changes are observable within the oocytes and the eggs become translucent due to the coalescence of yolk globules. Examination of ovaries undergoing active oogenesis indicates that oocyte development is not synchronous; that is, oocytes of varying sizes and in different phases of vitellogenesis are present."

References

Ball, J. N. 1960. Reproduction in female boney fishes. Symp. Zool. Soc. Lond. 1: 105-136.

Ballard, W. W. 1968. History of the hypoblast in *Salmo*. J. Exp. Zool. 168: 257-272.

Beams, H. W., and R. G. Kessel. 1973. Oocyte structure and early vitellogenesis in the trout, *Salmo gairdneri*. Am. J. Anat. 136: 105–122.

Braekevelt, C. R., and D. B. McMillan. 1967. Cyclic changes in the ovary of the brook stickleback, *Eucalia inconstans*. J. Morphol. 123: 373–395.

Brambell, F. W. R. 1960. Ovarian changes. Pages 377–542 *in* A. S. Parkes, ed. Marshall's physiology of reproduction, 3rd ed., vol. 1, part. 2. Longmans, Green, New York.

Brummett, A. R., J. N. Dumont, and J. R. Larkins. 1982. The ovary of *Fundulus heteroclitus*. J. Morphol. 173: 1–16.

Busson-Mabilot, S. 1973. Evolution des enveloppes de l'ovocyte et de l'oeuf chez un poisson teleosteen. J. Microsc. (Paris) 18: 23–44.

Chouinard, L. A. 1963. Sites of formation of the extra nucleole during early oocyte growth in the freshwater teleost, *Salvelinus fontinalis* Mitchill. Can. J. Zool. 41: 997-1010.

Combs, Ralph M. 1969. Embryogenesis, histology and organology of the ovary of *Brevoortia patronus*. Gulf Res. Rep. 2: 333–434.

Craig-Bennett, A. 1931. The reproductive cycle of the three-spined stickleback, *Gasterosteus aculeatus*. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 219: 197–279.

de Vlaming, V. L. 1972. Reproductive cycling in the estuarine gobiid fish, *Gillichthys mirabilis*. Copeia 1972: 278–291.

Dodd, J. M. 1960. Gonadal and gonadotropic hormones in lower vertebrates. Pages 417–482 *in* A. S. Parkes, ed. Marshall's physiology of reproduction, 3rd ed., vol. 1, part 2. Longmans, Green, New York.

Dutt, N. H. G. 1964. The yolk-nucleus in the oocytes of *Anabas scandens*. Q. J. Microscop. Sci. 105: 353–358.

Emel'yanova, N. G. 1980. Ultrastructure of oogonia and oocytes in silver carp. Sov. J. Dev. Biol. 10: 126–132. [Engl. Transl. Ontogenez]

Flugel, H. 1964. On the fine structure of the zona radiata of growing trout oocyte. Naturwissenschaften 22: 542.

Flugel, H. 1967. Licht- und elektronenmikroskopische Untersuchungen an Oozyten und Eiern einiger Knochenfische. Z. Zellforsch. Mikrosk. Anat. 83: 82–116.

Forberg, K. G. 1982. A histological study of development of oocytes in capelin, *Mallotus villosus villosus* (Muller). J. Fish Biol. 20: 143–154.

Franchi, L. L. 1962. The structure of the ovary. Pages 121–142 *in* S. Zuckerman, ed. The ovary, vol. 1. Academic Press, New York.

Funk, J. D., E. M. Donaldson, and H. M. Dye. 1973. Induction of precocious sexual development in female pink salmon *Oncorhynchus gorbuscha*. Can. J. Zool. 51: 493–500.

Gielen, J. T., H. J. T. Goos, J. Peute, R. A. van den Bosch, and P. G. W. J. van Oordt. 1982. The brain-pituitary-gonadal axis in the rainbow trout *Salmo gairdneri*: gonadal hormones and the maturation of gonadotropic cells. Cell Tissue Res. 225: 45–56.

Ginsburg, A. S. 1963. Sperm-egg association and its relationship to the activation of the egg in salmonid fishes. J. Embryol. Exp. Morphol. 11: 13–33.

Grier, H. J. 1981. Cellular organization of the testis and spermatogenesis in fishes. Am. Zool. 21: 345–357.

Hayes, F. R. 1949. The growth, chemistry and temperature relations of salmonid eggs. Q. Rev. Biol. 24: 281–308.

Hayes, F. R., and F. H. Armstrong. 1942. Physical changes in the constituent parts of developing salmon eggs. Can. J. Res. D20: 99–114.

Hayes, F. R., I. R. Wilmat, and D. A. Livingston. 1951. The oxygen consumption of the salmon egg in relation to development and activity. J. Exp. Zool. 116: 377–395.

Henderson, N. E. 1962. The annual cycle in the testes of the eastern brook trout, *Salvelinus fontinalis* (Mitchill). Can. J. Zool. 40: 631–641.

Hirio, O., and K. Yamamoto. 1966. Studies on the maturation of salmonid fishes – I. Change in the testis of chum salmon, *Oncorynchus keta*, during anadromous migration. Bull. Fac. Fish. Hokkaido Univ. 19: 173–184.

Hirio, O., and K. Yamamoto. 1970. Studies on the maturation of salmonid fishes – II. Change in the testis of masu salmon, *Oncorynchus masou*, during anadromous migration. Bull. Fac. Fish. Hokkaido Univ. 20: 252–260.

Hoar, W. S. 1955. Reproduction in teleost fish. Pages 5–24 *in* I. Chester Jones and P. Eckstein, eds. The comparative physiology of reproduction and the effects of sex hormones in vertebrates. No. 4. Mem. Soc. Endocrinol. Cambridge University Press, London.

Hoar, W. S. 1969. Reproduction. Pages 1–72 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 3. Academic Press, New York.

Hoffman, R., P. Wondrak, and W. Groth. 1980. Seasonal anatomical variations in the testes of European pike, *Esox lucius* L. J. Fish Biol. 16: 475–482.

Honma, Y., and E. Tamura. 1962. Seasonal changes in the gonads of the landlocked salmonid fish Ko-ayu, *Plecoglossus altivelis* Temminck et Schlegel. Jpn. J. Ichthyol. 9: 135–151.

Horstmann, E., and H. Breucker. 1972. Special mitochondria in the Leydig-cells of the teleost, *Trichogaster leeri* (Bleeker). Z. Zellforsch. Mikrosk. Anat. 134: 97–103.

Hurley, D. A., and K. C. Fisher. 1966. The structure and development of the external membrane in young eggs of the brook trout, *Salvelinus fontinalis* (Mitchill). Can. J. Zool. 44: 173–190.

Ivanova, S. A. 1956. Histological study of gonads of the pink salmon and the summer chum. Vopr. Ikhtiol. 6: 90–99.

James, M. F. 1946. Histology of gonadal changes in the bluegill, *Lepomis macrochirus* Rafinesque, and the largemouth bass, *Huro salmoides* L. J. Morphol. 79: 63–92.

Jones, J. W. 1940. Histological changes in the testis in the sexual cycle of male salmon parr (*Salmo salar* L. juv.). Proc. R. Soc. Lond. B. Biol. Sci. 128: 499–509.

Kendall, W. C. 1921. Peritoneal membranes, ovaries, and oviducts of salmonoid fishes and their significance in fish-cultural practices. Bull. U.S. Bur. Fish. 37: 185–208.

Kosaka, S. 1971. On the histological changes in the testis of precocious masu salmon parr. Bull. Tohoku Reg. Fish. Res. Lab 31: 163.

Knight, A. E. 1963. Embryonic and larval development of the rainbow trout, *Salmo gairdneri*. Trans. Am. Fish Soc. 92: 344–355.

Lagios, M. D. 1965. Seasonal changes in the cytology of the adenohypophysis, testes and ovaries of the black surfperch, *Embiotoca jacksoni*, a viviparous percomorph fish. Gen. Comp. Endocrinol. 5: 207–221.

Lang, I. 1981. Electron microscopic and histochemical study of the postovulatory follicles of *Perca fluviatilis* L. (Teleostei). Gen. Comp. Endocrinol. 45: 219–233.

Mahon, E. F., and W. S. Hoar. 1954. The early development of the chum salmon, *Oncorhynchus keta* (Walbaum). J. Morphol. 98: 1–46.

Manner, H. W., and C. M. Dewese. 1974. Early development of the fathead minnow *Pimephales promelas* Rafinesque. Anat. Rec. 180: 99–110.

Marshall, A. J., and B. Lofts. 1956. The Leydig-cell homologue in certain teleost fishes. Nature (Lond.) 177: 704–705.

Mathur, D. S. 1962. Seasonal variations in the ovary and testes of *Barbus stigma* (*Puntius sophore*). Zool. Pol. 12: 132–147.

McBride, J. R., and A. P. van Overbeeke. 1975. Effects of thiourea treatment on sexually maturing and gonadectomized male sockeye salmon *Oncorhynchus nerka*. J. Fish. Res. Board Can. 32: 11–19.

Nayyar, R. P. 1964. The yolk nucleus of fish oocytes. Q. J. Microsc. Sci. 105: 353–358.

Ohtsuka, E. 1960. On the hardening of the chorion of the fish egg after fertilization. III. The mechanism of chorion hardening in *Oryzias latipes*. Biol. Bull. (Woods Hole) 118: 120–128.

Oota, I., K. Yamamoto, K. Takano, and T. Sakaguchi. 1965. Studies on the maturing process of the rainbow trout, *Salmo gairdnerii irideus* – II. Maturation of the testis of a one-year old fish. Bull. Jpn. Soc. Sci. Fish. 31: 597–605.

Parker, J. B. 1943. The reproductive system of the brown trout (*Salmo fario*). Copeia 1943: 90–91.

Partle, J. M. 1955. Histological studies on albacore (*Thunnus alalunga*) gonads from the Eastern Pacific. J. Fish. Res. Board Can. 12: 61–67.

Riehl, R. 1977*a*. Light and electromicroscopical investigations about structure and development of microphiles of *Noemacheilus barbatu* (L.) and *Gobio gobio* (L.) (Pisces, Teleostei). Zool. Anz. 198: 313–327.

Riehl, R. 1977*b*. Histochemical and ultrahistochemical investigations of the oocytes of *Noemacheilus barbatu* (L.) and *Gobio gobio* (L.) (Pisces, Teleostei). Zool. Anz. 198: 328–354.

Robb, A. P. 1982. Histological observations on the reproductive biology of the haddock, *Melanogrammus aeglefinus* (L.). J. Fish Biol. 20: 397–408.

Robertson, O. H. 1958. Accelerated development of testis after unilateral gonadectomy, with observations on normal testis of rainbow trout. U.S. Fish Wild. Serv., Fish. Bull. 58: 9–30.

Robertson, O. H., S. Hane, B. C. Wexler, and A. P. Rinfret. 1963. The effect of hydrocortisone on immature rainbow trout *Salmo gairdneri*. Gen. Comp. Endocrinol. 3: 422–436.

Robertson, O. H., M. A. Krupp, S. F. Thomas, C. G. Favour, S. Hane, and B. C. Wexler. 1961. Hyperadrenocorticism in spawning migratory and nonmigratory rainbow trout (*Salmo gairdneri*); comparison with Pacific salmon *Oncorhynchus*. Gen. Comp. Endocrinol. 1: 473–484.

Ruby, S. M., and D. B. McMillan. 1970. Cyclic changes in the testis of the brook stickleback *Eucalia inconstans* (Kirtland). J. Morphol. 131: 447–466.

Sato, M. 1960. The hatching and hatching glands of catfish, *Parasilurus asotus* L. Sci. Rep. Hirosaki Univ. 7: 48–56.

Takashima, F., R. Patino, and M. Nomura. 1980. Histological studies on the sex differentiation in rainbow trout. Bull. Jpn. Soc. Sci. Fish. 46: 1317.

Tsuneki, K., and A. Gorbman. 1977*a*. Ultrastructure of the testicular interstitial tissue of the hagfish *Eptatretus stouti*. Acta Zool. (Stockh.) 58: 17–25.

Tsuneki, K., and A. Gorbman. 1977*b*. Ultrastructure of the ovary of the hagfish *Eptatretus stouti*. Acta Zool. (Stockh.) 58: 27–40.

Upadhyay, S. N., and S. S. Guraya. 1971. Histochemical observations on the interstitial tissues of fish testes. Gen. Comp. Endocrinol. 16: 504–510.

van den Hurk, R., and J. Peute. 1979. Cyclic changes in the ovary of the rainbow trout, *Salmo gairdneri*, with special reference to sites of steroidogenesis. Cell Tissue Res. 199: 289–306.

van den Hurk, R., and G. A. Slof. 1981. A morphological and experimental study of gonadal sex differentiation in the rainbow trout, *Salmo gairdneri*. Cell Tissue Res. 218: 487–497.

Vernier, J. M. 1969. Table chronologique du developpement embryonnaire de la truite arc-en-ciel, *Salmo gairdneri* Rich. Ann. Embryol. Morphol. 2: 495–520.

Wallace, R. A., and K. Selman. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21: 325–343.

Weisel, G. F. 1943. A histological study of the testes of the sockeye salmon (*Oncorhynchus nerka*). J. Morphol. 73: 207–229.

Weisel, G. F. 1949. The seminal vesicles and testis of *Gillichthys*, a marine teleost. Copeia 1949: 101–110.

Wiebe, J. P. 1968. The reproductive cycle of the viviparous seaperch, *Cymatogaster aggregata*. Can. J. Zool. 46: 1221–1234.

Yamamoto, K. 1964. Electron microscopy of fish development. III. Changes in the ultrastructure of the nucleus and cytoplasm of the oocyte during its development in *Oryzias latipes*. J. Fac. Sci. Univ. Tokyo. 10: 335–346

Yamamoto, K., I. Oota, K. Takano, and T. Ishikawa. 1965. Studies on the maturing process of the rainbow trout, *Salmo gairdnerii irideus* – I. Maturation of the ovary of a one-year old fish. Bull. Jpn. Soc. Sci. Fish. 31: 123–132.

Zeitoun, I. H., and P. I. Tack. 1974. The embryology of the coho salmon, *Oncorhynchus kisutch* (Walbaum). Trans. Am. Fish. Soc. 103: 371–375.

Zotin, A. I. 1958. The mechanism of hardening of the salmonid egg membrane after fertilization or spontaneous activation. J. Embryol. Exp. Morphol. 6: 546–568.

Plate 51. Testis

Fig. 1. Section of testis of 14-month-old rainbow trout, showing an early stage of spermatogenesis. × 250.

- a. Testicular sheath
- b. Primary spermatocytes

Fig. 2. Detail of Fig. 1. × 560.

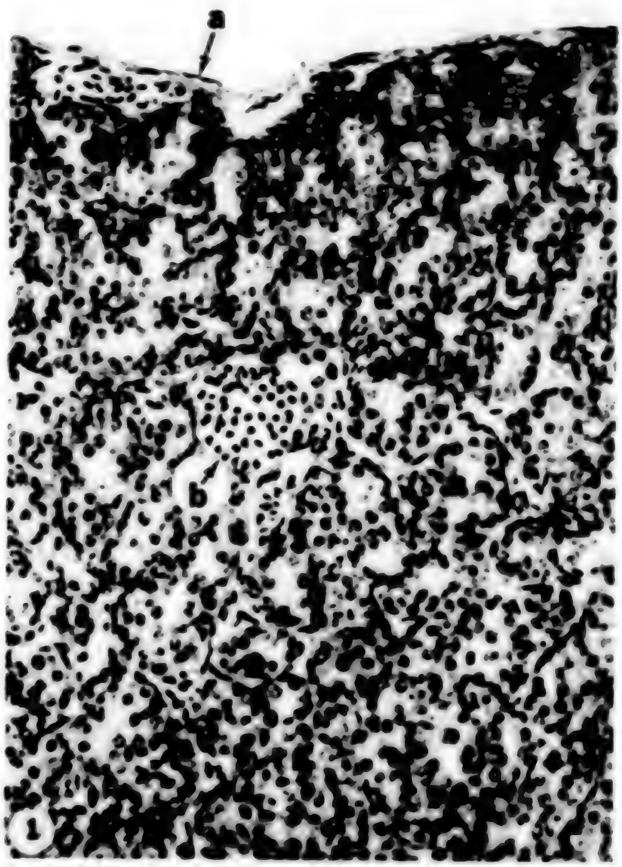
- a. Spermatocyte in metaphase
- b. Lobule of primary spermatocytes
- c. Macrophage adjacent to lobule wall
- d. Cyst of primordial germ cells

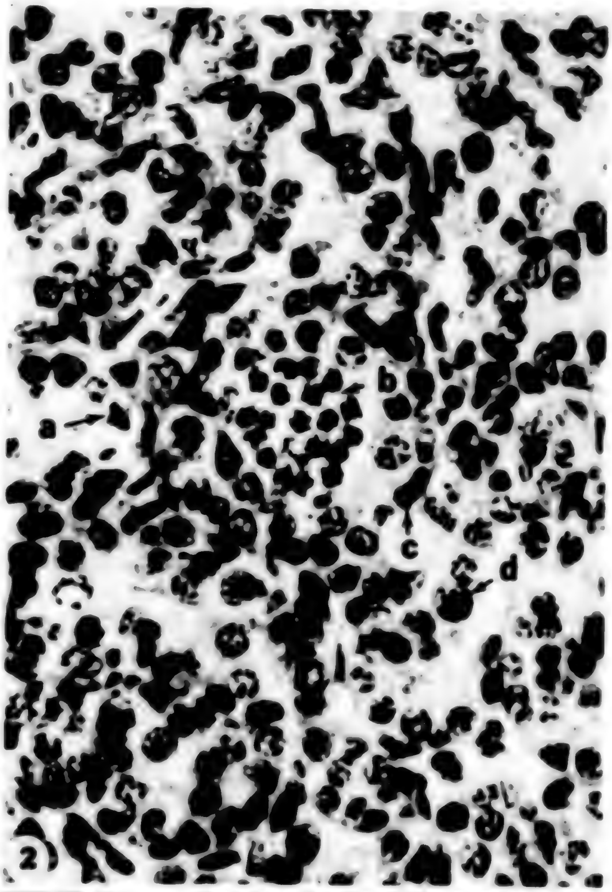
Fig. 3. Section of testis of 19-month-old rainbow trout. × 250.

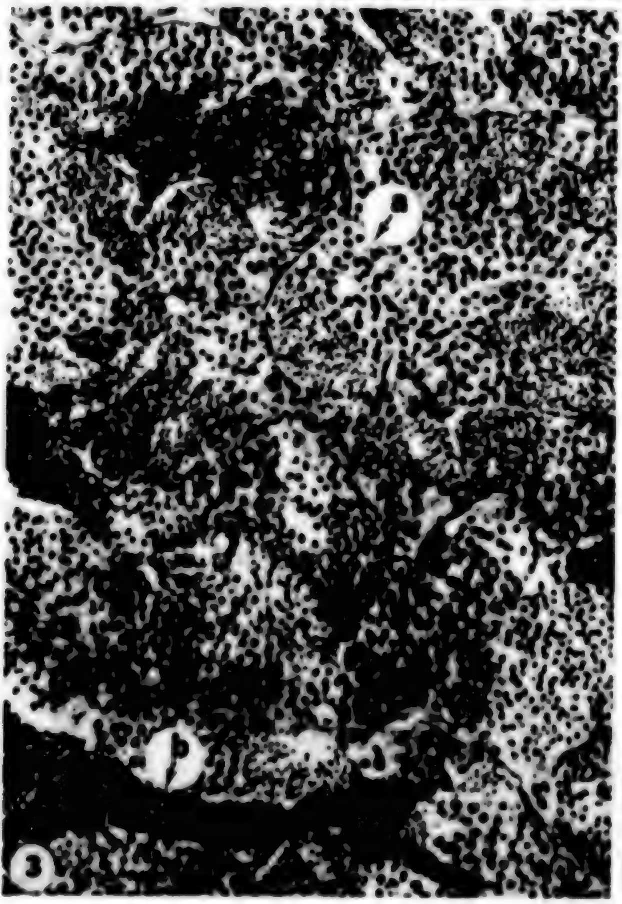
- a. Lobule containing both secondary spermatocytes and spermatids
- b. Mature sperm (spermatozoa) in lumen of lobule

Fig. 4. Detail of Fig. 3. × 560.

- a. Primary and secondary spermatocytes
- b. Spermatids
- c. Spermatozoa


a
b
1


a
b
c
d
2


a
b
3

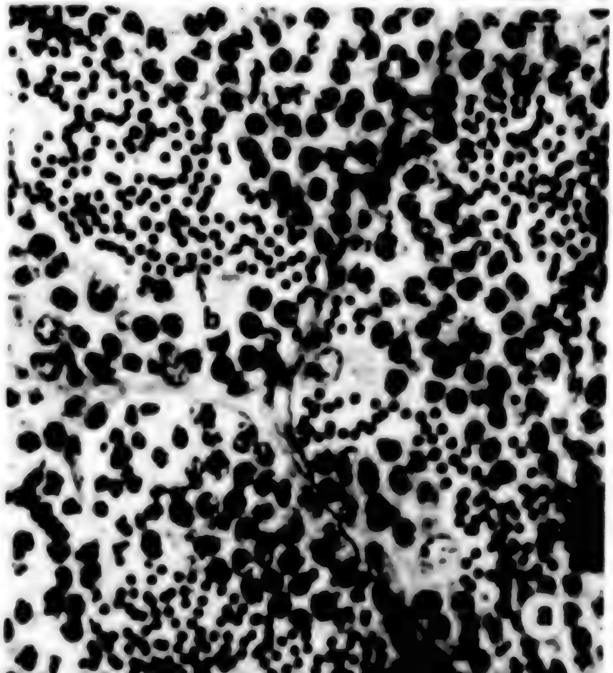

b
c
4

Plate 52. Ovary

Fig. 1. Ovary of 14-month-old rainbow trout. × 50.

- a. Oocyte containing numerous vacuoles and a deeply staining nucleus
- b. Nucleus surrounded by many vacuoles
- c. Small oocytes surrounded by still smaller oocytes

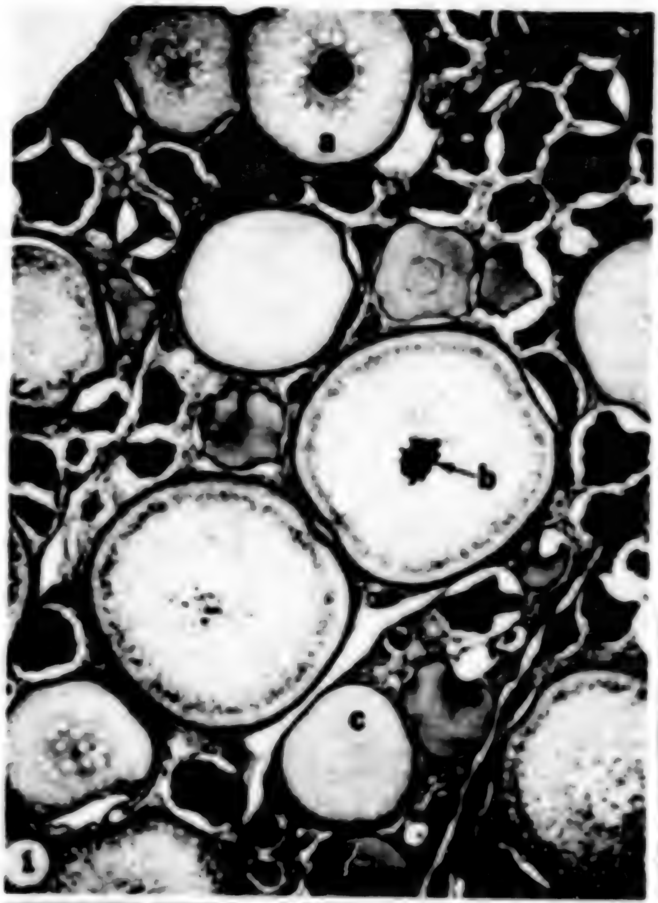
Fig. 2. Detail of three oocytes. × 300.

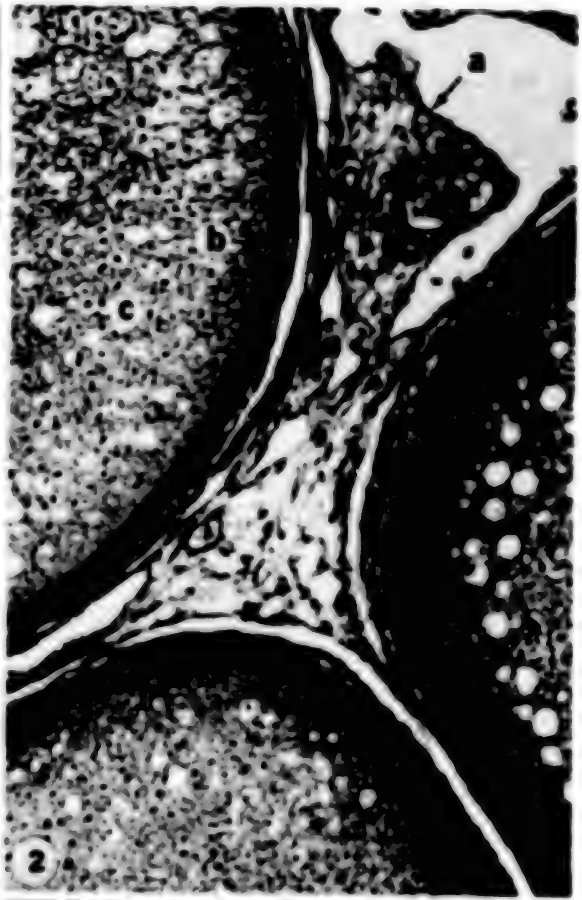
- a. Stroma of connective tissue binding the oocytes into an ovigerous lamella
- b. Three layers surround the oocyte: first the zona radiata, second the follicle, and outermost the vascularized theca.
- c. Yolk

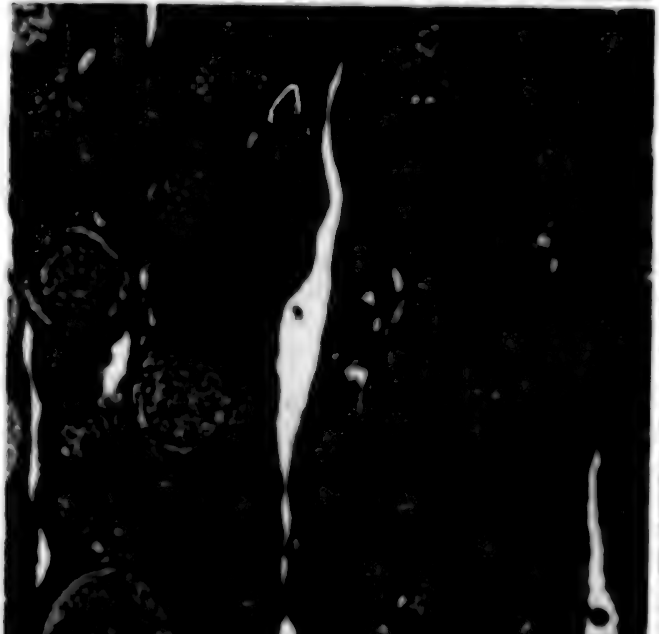
Fig. 3. Two ovigerous lamellae. The larger oocytes presumably will mature, and the smaller ones may be resorbed. × 40.

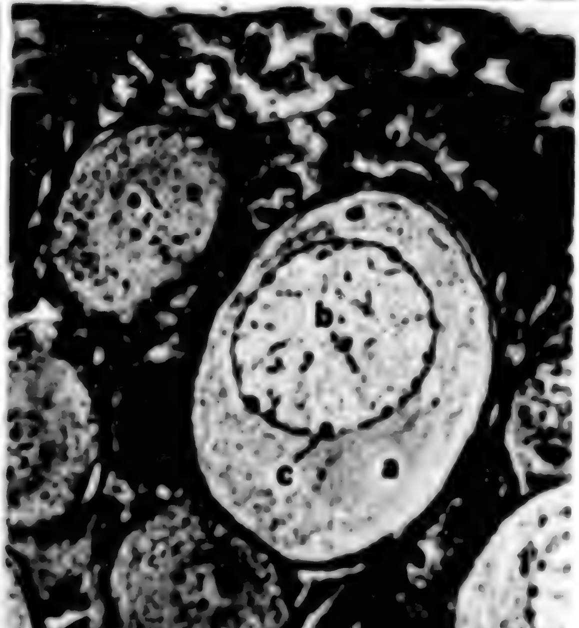
Fig. 4. Detail of lamella, showing one oocyte that presumably would mature and several smaller ones that might be resorbed. × 700.

- a. Yolk
- b. Nucleus
- c. Nucleolus


a
b
c
1


a
b
c
2


3


b
c
a
4

Chapter XIII

Endocrine System

The basic components of the teleost endocrine system are the same as those found in higher vertebrates. The system does, however, have tissues such as the corpuscles of Stannius, urophysis, and pseudobranch that are characteristic only of teleosts (Roberts 1978). Harder (1975) listed 15 tissues in which endocrine activity occurs: pituitary, thyroid, interrenal, chromaffin, corpuscles of Stannius, saccus vasculosus, ultimobranchial, islets of Langerhans (Chapter IV), interstitial cells of the digestive tract (Chapter IV), pseudobranchs (Chapter V), thymus (Chapter VIII), juxtaglomerular cells of the kidney (Chapter IX), urophysis (Chapter X), pineal (Chapter XI), and gonads (Chapter XII).

The approximate location of most of these tissues, which can be observed histologically, is shown in Diagram 7. The first seven tissues listed have not been discussed in preceding chapters and are discussed here.

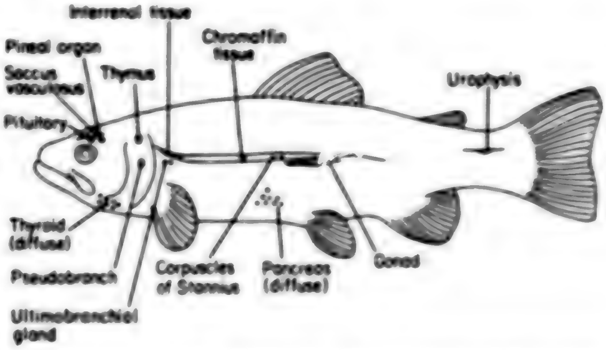


Diagram 7. Location of tissues in which endocrine activity occurs in teleosts. (Redrawn from Wedemeyer et al. 1976)

Pituitary Gland (Hypophysis)

The terminology used here is that suggested for the adenohypophysial region of the teleost pituitary gland by Gorbman (1965), which is currently accepted by most investigators (McBride and van Overbeeke 1967, 1969; Nagahama 1973; Schreibman et al. 1977 Boddingius 1975, 1976).

The pituitary gland or hypophysis is ventral to the diencephalon and connected to it by a short infundibulum (Plate 53, Fig. 1; Plate 54, Fig. 1). The two major components are the neurohypophysis and the adenohypophysis. Embryologically the neurohypophysis is formed by the vertical extension of the diencephalon, and the adenohypophysis is derived from the dorsal projection of the roof of the buccal cavity (Ball and Baker 1969; Schreibman et al. 1973; Grizzle and Rogers 1976). The adenohypophysis is generally considered to be homologous to the same organ in mammals (van Overbeeke and McBride 1967).

The adenohypophysis synthesizes, stores, and passes several hormones into general circulation. The neurohypophysis is believed to be responsible for controlling the adenohypophysis, osmoregulation, and some aspects of reproduction (Anderson and Mitchum 1974; Grizzle and Rogers 1976). The functions of hormones produced by the hypophysis are numerous; some are well established, some are tentatively established, and no doubt some are still unrecognized. Comprehensive treatises and supporting literature citations on the subject have been published by Bern (1967), Ball (1969), Ball and Baker (1969), Nagahama (1973), and Schreibman et al. (1973).

Neurohypophysis

Histologically, the neurohypophysis appears fibrous since it consists of glial cells (pituicytes) and three types of neurosecretory fibers originating in the hypothalamus of the brain and blood vessels. The secretory cells of the neurohypophysis lie within the floor of the diencephalon and their axons descend into the infundibulum and interdigitate with all areas of the pituitary (Schreibman et al. 1973; Plate 53; Plate 54, Figs. 1 and 2). A detailed discussion of the tissue may be found in Perks' (1969) report.

Adenohypophysis

The adenohypophysis, histologically, consists of three major areas (Gorbman 1965): the rostral pars distalis (proadenohypophysis), proximal pars distalis (caudal pars distalis or mesoadenohypophysis), and pars intermedia (metaadenohypophysis). Cells in each of these areas can usually be identified by their arrangement as well as by their morphological and staining characteristics. Several staining methods have been shown to be useful in differentiating the various cell types: Bouin-Hollande fixation followed by Masson's trichrome (Plate 55), Mallory-Heidenhain, Heidenhain-Azen, and periodic acid-Schiff (PAS)-orange G-light green (Plate 56).

The rostral pars distalis is composed mainly of prolactin cells (Plates 54, 55, 56). These cells in many of the salmonids, including trout, are elongated and form follicles and are seen predominantly in the anterior area of the adenohypophysis. Ball and Baker (1969) suggested that prolactin hormone plays an important role in osmoregulation.

Other functions in other species of fish have also been suggested (Schreibman et al. 1973). Adrenocorticotrophic (ACTH) cells or corticotrophs, which stimulate the release of interrenal steroids from the anterior kidney, can also be seen in the area (Oguri 1971).

In the proximal pars distalis three cell types can be seen: somatotropin (growth hormone), gonadotropin, and thyrotropin (thyroid stimulating hormone). In Masson's trichrome stain, somatotropin cells appear dark magenta (Plate 54, Fig. 3) and in PAS-orange G-light green they stain orange G (Plate 55). In most teleosts the gonadotropins are usually found in the proximal pars distalis, but in trout they are also in the rostral region (Ball and Baker 1969). It is often difficult to distinguish between gonadotropin and somatotropin cells in Masson's or PAS-orange G-light green stains (Plates 54, 55) because both are basophilic and PAS positive (Grizzle and Rogers 1976).

The pars intermedia is in the most posterior of the three adenohypophysis regions. In salmonids it frequently occupies nearly two-thirds of the area and is reported to have only one type of cell, the melanophore stimulating hormone cell (Ball and Baker 1969; Schreibman et al. 1973).

Thyroid Gland

The thyroid tissue in teleosts consists of glandular follicles scattered about the ventral aorta and branchial arteries that supply the gills (Plate 57). The center of each follicle is filled with colloid. The surrounding epithelial cells may be flattened, cuboidal, or columnar, depending on their activity. The colloid is a reserve of the protein-bound form of the thyroid hormone (Anderson and Mitchum 1974). The staining characteristics of the colloid are indicators of glandular activity. Eosinophilic colloid is associated with the flattened, squamous, relatively inactive epithelium. In the active gland with tall, columnar cells, the colloid tends to be more basophilic and often contains vacuole-like spaces. The area in which the follicles lie is highly vascularized. The size of the follicular cells varies considerably with altered physiological states. The vacuoles may occasionally occur within the follicular material (Plate 56, Fig. 3).

Thyroxine, the secretion of the thyroid gland, is essential for many functions. Gorbman and Bern (1962) stated that a far greater number of organ systems and metabolic processes are affected by the thyroid hormones than by any of the other endocrine hormones. In salmonids, thyroxine is essential for maturation; injections of thyroxine induce smoltification. Thyroxine is also essential for proper functioning of the nervous system. The best-known function is the accumulation and storage of iodine. The deficiency of this element in the water and diet of salmonids often results in serious thyroid goiter. The use of isotopes of iodine has made it possible to trace thyroid products throughout the fish's body. The pituitary controls the thyroid gland through its secretion of the thryoid stimulating hormone.

Adrenal Gland

Interrenal Tissue

The interrenal tissue is located in the head (hematopoietic) kidney in close association with the cardinal veins and the chromaffin tissue that lines these veins. It is homologous to the adrenal cortex of mammals and serves primarily as the cortical steroid producing tissue (Nandi 1962; Yoakim and Grizzle 1980). The proximity of these two cell types leads to some confusion but they can be distinguished even in sections stained with hematoxylin and eosin. The histochemical differences are more evident when the sections are stained with Masson's trichrome. When this technique is used, the cytoplasm of the interrenal cells is stained lavender and the nuclei are stained a darker purple; in contrast, the chromaffin cells show almost no coloration of the cytoplasm and their nuclei are lightly stained. The morphology of the interrenal follicles and of the cells themselves is very distinctive (Plate 57, Figs. 1 and 2). They are embedded in the hematopoietic parenchyma and usually assume a rounded or oval shape. The follicles may occur along the minor blood vessels of the head kidney, where they assume a long, tubular form. The nuclei of the interrenal cells are noticeably uniform, small, and subspherical. The chromaffin nuclei are not uniform in size or shape.

Chromaffin Tissue

Chromaffin cells are found in the head (hematopoietic) portion of the trout kidney, where they are closely associated with the interrenal tissue (Plate 57, Fig. 3). These cells were so named because of their affinity for chromate "stains" (Plate 58). The potassium dichromate-chromate method of Hillarp and Hokfelt (1955) was used for the chromaffin reaction. The cells are homologous to the cells of the mammalian adrenal medulla (Yoakim and Grizzle 1980). The granules in these cells are usually brownish; the interrenal cells lack such granules. In sections of kidneys stained with Masson's trichrome, the chromaffin cells appear either colorless or have a faint basic reaction, whereas the interrenal cells are eosinophilic and appear slightly pink. The nuclei of the two types of cells have characteristic features. The chromaffin nuclei are oval or irregular in shape and are larger than the nuclei of the interrenal cells, which are round or oval and have a well-defined nucleolus and chromatin particles. The location of the chromaffin cells differs from that of the interrenal cells: whereas the chromaffin cells lie along the major blood vessels of the head kidney, the interrenal cells are usually scattered throughout the hematopoietic tissue.

Both epinephrine and norepinephrine are produced by the chromaffin cells. The functions attributed to these hormones have not been completely defined; however, they are known to play a role in the stress response-defensive "fight or flight" reactions. These defense reactions also include rapid changes in blood sugar level, cardiac output, and blood vessel diameter.

Corpuscles of Stannius

The glandular bodies or corpuscles described by Stannius in 1829 are usually found on the ventral surface of the mesonephros. In salmonid fishes they are light-colored, oval clusters of cells, differing in number and location (Plates 59, 60). Anderson and Mitchum (1974) recorded a maximum of 14 corpuscles of Stannius, but in rainbow trout the number commonly ranges from 2 to 6. They arise by budding from the pronephric duct. Each corpuscle is divided into a variable number of lobules by walls of connective tissue projecting inward from the encapsulating membrane (Plate 60). The lobules are composed of convoluted "cords" of parenchymal cells (Carpenter and Heyl 1974). In salmonids these parenchymal cells are of two types, based on their staining reaction at the light microscope level and on certain microsomal differences when they are photographed by electron microscopy. Krishnamurthy and Bern (1969) characterized the two types as "granular" and "agranular." The granular cells are periodic acid-Schiff positive; the agranular cells are negative. The granules appear to be secretory, but the function of the secretion is not well understood. Various workers have found evidence of a calcium regulatory function, but the pathway has not been clearly defined. Chester Jones et al. (1969) presented evidence that the secretions of the corpuscles perform a role that is distinct from that of the adrenal cortex, but both systems may act on the kidney, supplementing each other in electrolyte homeostasis. Chan (1972) found that the cells were active in salmon smolts and inactive in adults. The ultrastructure suggested that they were involved in production of protein hormones rather than steroids. Photographs by Lopez (1969) showed histological changes in the corpuscles at different times in the life cycle of the Atlantic salmon (*Salmo salar*).

Saccus Vasculosus

The saccus vasculosus (Plate 53, Fig. 1; Plate 54, Fig. 1) is a saclike protrusion of the diencephalon's caudal infundibular wall, located directly posterior to the pituitary (Jansen and Flight 1969; Jansen 1975). Essentially, the saccus is an organ whose walls are infolded at many points. The lumen of the sac appears empty in paraffin embedded preparations, and blood lies within the folds (Plate 61, Fig. 2). The nuclei of the coronet cells are separated from the blood-filled "crevices" in the sac by the basal membrane. The proximity of the coronet nuclei and the blood suggest a need for high oxygenation. The distal portion of the coronet cell may have a storage function. Hairlike extensions from the distal end of the coronet cells support globules of different sizes (Plate 61, Figs. 3 and 4). It seems entirely possible that the globules consist of some substance being secreted into the lumen of the organ. Since the lumen of the saccus is actually an extension of the third ventricle of the brain, it has been suggested that the secretion of the coronet cells produces a neuro-stimulation. Three functions have been attributed to the saccus vasculosus: sensory, secretory, and absorptive (Jansen and Flight 1969).

Ultimobranchial Gland

The ultimobranchial glands are found within the transverse septum; the connective tissue covers the ventral surface of the esophagus as it emerges through the pericardial septum, just dorsal to the liver attachment (Plate 62). Although in other species it may occur as a single gland, it is paired in trout (Robertson 1969). In yearling or younger rainbow trout the follicles are difficult to locate. Histologically, the individual gland cells are tall-columnar (6 × 65 μm), and each has an elongate, oval nucleus situated in the basal one-third of the cell. Pang (1971, 1973) suggested that this gland is the source of calcitonin, which plays a role in calcium regulation and may also be involved in osmoregulation.

References

The Pituitary Gland

Anderson, B. G., and D. L. Mitchum. 1974. Atlas of trout histology. Wyo. Game Fish Dep. Bull. 13. 110 pp.

Baker, B. I. 1964. Pituitary-thyroid relationship during development in the teleost *Herichthys cyanoguttatus*: a histophysiologic study. Gen. Comp. Endocrinol. 4: 164–175.

Baker, B. I. 1969. The response of teleost pituitary thyrotrophs to thyroxin *in vitro*—a histological study. Gen. Comp. Endocrinol. 12: 427–437.

Ball, J. N. 1969. Prolactin (fish prolactin or paralactin) and growth hormone. Pages 207–240 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

Ball, J. N., and B. I. Baker. 1969. The pituitary gland: anatomy and histophysiology. Pages 1–110 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

Bargmann, W. 1953. Uber das Zwischenhirn-hypophysensystem von Fischen. Z. Zellforsch. Mikrosk. Anat. 38: 275–298.

Benjamin, M. 1979*a*. The cell types in the adenohypophysis of the marine teleost *Crenilabrus melops*. Acta Zool. (Stockh.) 60: 105–113.

Benjamin, M. 1979*b*. Comparative ultrastructural studies on the prolactin cells in the pituitary of nine-spined sticklebacks, *Pungitius pungitius* L., with and without adenohypophyseal cysts. Zoomorphologie 93: 125–135.

Bern, H. A. 1967. Hormones and endocrine glands of fishes. Science 158: 455–462.

Billenstien, D. C. 1963. Neurosecretory material from the nucleus lateralis tuberis in the hypophysis of the eastern brook trout *Salvelinus fontinalis*. Z. Zellforsch. Mikrosk. Anat. 59: 507–512.

Boddingius, J. 1975. The cell types of the adenohypophysis in rainbow trout (*Salmo irideus*). A histological study. Holywell Press Ltd., Oxford. 130 pp.

Boddingius, J. 1976. The influence of social rank on adenohypophysial cell activity in *Salmo irideus*. Cell Tissue Res. 170: 383–414.

Boddingius, J., and E. M. Fallaux. 1970. Argyrophil adenohypophysial cells in the rainbow trout (*Salmo irideus*), demonstrated simultaneously with chromophil cells and with intracellular argyrophil fibrils by a new technique. Neth. J. Zool. 20: 291–297.

Chestnut, C. W. 1970. The pituitary gland of coho salmon (*Oncorhynchus kisutch* Walbaum) and its function in gonad maturation and thyroid activity. Ph.D. Thesis. Simon Fraser University, Burnaby, B.C.

Chiba, A., and Y. Honma. 1974. Cell types in the adenohypophysis of the puffer, *Fugu stictonotus*, with special reference to the basophils in the pars distalis. Arch. Histol. Jpn. 36: 291–305.

Chiba, A., Y. Honma, S. Yoshie, and Y. Ojima. 1979. Histological observation of some of the endocrine glands in the sterile carp-funa hybrid (F_1), with special reference to the hypophysis. Arch. Histol. Jpn. 42: 305–318.

Clarke, W. C., and Y. Nagahama. 1977. Effect of premature transfer to sea water on growth and morphology of the pituitary, thyroid, pancreas, and interrenal in juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Zool. 55: 1620–1630.

Cook, H., and A. P. van Overbee[illegible]trastructure of the beta cells in the pituitary gland of a[illegible] migratory sockeye (*Oncorhynchus nerka*). Can. J. Zool. 47: 937–941.

Cook, H., and A. P. van Overbeeke. 1972. Ultrastructure of the pituitary gland (pars distalis) in sockeye salmon (*Oncorhynchus nerka*) during gonad maturation. Z. Zellforsch. Mikrosk. Anat. 130: 338–350.

Dodd, J. M., and T. Kerr. 1963. Comparative morphology and histology of the hypothalamo-neurohypophysial system. Symp. Zool. Soc. Lond. 9: 5–27.

Ekengren, B., K. Lindahl, and G. Fridberg. 1978. Immunocytology and innervation of the gonadotropic cells in the teleost fish *Rutilus rutilus*. Acta Zool. (Stockh.) 59: 125–133.

Ekengren, B., J. Peute, and G. Fridberg. 1978*a*. The distribution and nature of gonadotropic cells in the rostral pars distalis of the Atlantic salmon, *Salmo salar*. Ann. Biol. Anim. Biochem. Biophys. 18: 799–804.

Ekengren, B., J. Peute, and G. Fridberg. 1978*b*. Gonadotropic cells in the Atlantic salmon, *Salmo salar*. An experimental immunocytological, electron microscopical study. Cell Tissue Res. 191: 187–203.

Ethridge, L., and M. Benjamin. 1977. The time-sequence of response of the prolactin cells of the freshwater teleost, *Poecilia reticulata*, to an altered environmental salinity. Cell Tissue Res. 182: 371–382.

Follenius, E. 1965. Bases structurales et ultrastructurales des correlations diencephalo-hypophysaires chez les Selaciens et les Teleosteens. Arch. Anat. Microsc. Morphol. Exp. 54: 195–216.

Fontaine, M., and M. Olivereau. 1975. Some aspects of the organization and evolution of the vertebrate pituitary. Am. Zool. 15: 61–79.

Fridberg, G., and B. Ekengren. 1977. The vascularization and the neuroendocrine pathways of the pituitary gland in the Atlantic salmon, *Salmo salar*. Can. J. Zool. 55: 1284–1296.

Gorbman, A. 1965. Endocrine terminologic usage. Gen. Comp. Endocrinol. 5: 129–130.

Gorbman, A., and H. S. Bern. 1962. A textbook of comparative endocrinology. Wiley and Sons Inc., New York. 468 pp.

Grizzle, J. M., and W. A. Rogers. 1976. Anatomy and histology of the channel catfish. Auburn University Agricultural Experiment Station, Auburn, Alabama. 94 pp.

Gupta, O. P., and R. K. Shrivastava. 1971. Studies on the location, anatomy and histology of the endocrine glands of *Xenentodo ancila* (Ham.). Okajimas Folia Anat. Jpn. 48: 189–203.

Haider, S., and A. F. Sathyanesan. 1972. Comparative study of the hypothalamoneurohypophyseal complex in some Indian freshwater teleosts. Acta Anat. 81: 202–224.

Hane, W., K. Bergehoff, and D. K. O. Chan. 1967. Histological observations on pituitary ACTH-cells, adrenal cortex and the corpuscles of Stannius of the European eel (*Anguilla anguilla* L.). Gen. Comp. Endocrinol. 9: 64–75.

Harder, W. 1975. Anatomy of fishes. E. Schweizerbart'sche Verlagsbuchhanglung (Nagele u. Obermiller) Stuttgart. Part I. 612 pp. Part II. 132 pp. (Transl. from German)

Henderson, N. E. 1969. Structural similarities between the neurohypophyses of brook trout and tetrapods. Gen. Comp. Endocrinol. 12: 148–153.

Higgs, D. A., E. M. Donald, H. M. Dye, and J. R. McBride. 1976. Influence of bovine growth hormone and L-thyroxine on growth, muscle composition, and histological structure of the gonads, thyroid, pancreas, and pituitary of coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33: 1585–1603.

Honma, Y., and S. Yoshie. 1974. Studies on the endocrine glands of a salmonid fish, the ayu, *Plecoglossus altivelis* Temminck et Schlegel – IX. Seasonal changes in the cells of the adenohypophysis, especially the prolactin producing cells. Arch. Histol. Jpn. 36: 237–250.

Jasinski, A. 1962. Structure and vascularisation of the pituitary body of teleosts. Part II. The rainbow trout (*Salmo irideus* Gibb.), pike-perch (*Lucioperca lucioperca* L.), burbot (*Lota lota* L.) and pond loach (*Misgurnus fossilis* L.). Acta Biol. Cracov., Ser. Zool. 5: 67–93.

Jose, T. M., and A. G. Sathyanesan. 1977. Pituitary cytology of the Indian carp *Labeo rohita* (Ham.). Anat. Anz. 142: 410–423.

Jose, T. M., and A. G. Sathyanesan. 1980. Pituitary cytology of the freshwater teleost *Anabas testudineus* (Bloch). Z. Mikrosk. Anat. Forsch. (Leipz.) 94: 123–132.

Joy, K. P., and A. G. Sathyanesan. 1979. Functional cytology of the pituitary gland of the teleost *Clarias batrachus* (L.). Endokrinologie 73: 82–90.

Lagios, M. D. 1973. Follicle boundary cells in the adenohypophysis of the chondrostean and holostean fishes: an ultrastructural study of their relationship to the follicular lumen, to endocrine cells, and to the hypophysial cleft. Gen. Comp. Endocrinol. 20: 362–376.

Lal, B. 1964. Morphological, histological and histochemical studies of the pituitary gland of *Cirrhina mrigala* Hamilton. Proc. Indian Acad. Sci. (B) 59: 297–317.

Leatherland, J. F. 1972. Histophysiology and innervation of the pituitary gland of the goldfish, *Carassius auratus* L.: a light and electron microscope investigation. Can. J. Zool. 50: 835–844.

Leatherland, J. F., and L. Lin. 1975. Activity of the pituitary gland in embryo and larval stages of coho salmon, *Oncorhynchus kisutch*. Can. J. Zool. 53: 297–310.

Leatherland, J. F., and R. A. Sonstegard. 1981. Thyroid function, pituitary structure and serum lipids in Great Lakes coho salmon, *Onchorhynchus kisutch* Walbaum; "jacks" compared with sexually immature spring salmon. J. Fish Biol. 18: 643–653.

Lehri, G. K. 1970. Correlative cyclical changes in the pituitary gland and the testis of a catfish, *Clarias batrachus* (Linn.). Mikroskopie 26: 50–56.

McBride, J. R., and A. P. van Overbeeke. 1969. Cytological changes in the pituitary gland of the adult sockeye salmon (*Oncorhynchus nerka*) after gonadectomy. J. Fish. Res. Board Can. 26: 1147–1156.

McBride, J. R., and A. P. van Overbeeke. 1975. Effects of thiourea treatment on sexually maturing and gonadectomized male sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 32: 11–29.

McKeown, B. A., and A. P. van Overbeeke. 1971. Immunihistochemical identification of pituitary hormone producing cells in the sockeye salmon (*Oncorhynchus nerka*, Walbaum). Z. Zellforsch. Mikrosk. Anat. 112: 350–362.

McKeown, B. A., and J. F. Leatherland. 1973. Fine structure of the adenohypophysis in immature sockeye salmon, *Oncorhynchus nerka*. Z. Zellforsch. Mikrosk. Anat. 140: 459–471.

Moiseeva, E. G. 1971. Identification and some morphological features of proadenohypophyseal cells of Gobiidae. Dokl. Akad. Nauk SSSR Ser. Biol. 197: 501–503.

Nagahama, Y. 1973. Histo-physiological studies on the pituitary gland of some teleost fishes, with special reference to the classification of hormone-producing cells in the adenohypophysis. Bull. Fac. Fish. Hokkaido Univ. 21: 1–53.

Nagahama, Y., and K. Yamamoto. 1970*a*. Morphological studies on the pituitary of the chum salmon, *Oncorhynchus keta* (I). Fine structure of the adenohypophysis. Bull. Fac. Fish. Hokkaido Univ. 20: 293–302.

Nagahama, Y., and K. Yamamoto. 1970*b*. Morphological studies on the pituitary of the chum salmon, *Oncorhynchus keta* (II). Changes of the prolactin cells during the life-cycle. Bull. Fac. Fish. Hokkaido Univ. 21: 169–177.

Oguri, M. 1971. A histological study on the ACTH cells in the pituitary glands of freshwater teleosts. Bull. Jpn. Soc. Sci. Fish. 37: 577–584.

Olivereau, M. 1954. Hypophyse et glande thyroide chez les Poissons. Etude histophysiologique de quelques correlations endocriniennes, en particulier chez *Salmo salar* L. Ann. Inst. Oceanog. (Monaco) (N.S.) 29: 95–296.

Olivereau, M. 1971. The histological structure of some endocrine glands of the eel following autotransplantation of the hypophysis. Acta Zool. (Stockh.) 52: 69–83.

Olivereau, M. 1972. Identification of the thyrotrophic cells in the hypophysis of the Pacific salmon (*Oncorhynchus tshawytscha* Walbaum) after radiothyroidectomy. Z. Zellforsch. Mikrosk. Anat. 128: 175–187.

Olivereau, M. 1976. Les cellules gonadotropes hypophysaires du saumon de l'Atlantique: unicite ou dualite? Gen. Comp. Endocrinol. 28: 82–95.

Olivereau, M. 1977. Gonadotrophic cells in teleost fish. Inv. Pesq. 41: 67–68.

Olsson, R. 1968. Evolutionary significance of the "prolactin" cells in teleostean fishes. Nobel Symp. 4: 455–472.

Peter, R. E. 1973. Neuroendocrinology of teleosts. Am. Zool. 13: 743–755.

Perks, A. M. 1969. The neurohypophysis. Pages 112–205 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

Pickford, G. E., and J. W. Atz. 1957. The physiology of the pituitary glands of fishes. New York Zoological Society, N.Y. 613 pp.

Rao, P. D. P. 1972. Histology of the pituitary gland of six species of fishes belonging to the genus *Mystus* Scopoli (Teleostomi). Anat. Anz. 130: 347–361.

Roberts, R. J., editor. 1978. Fish pathology. Bailliere Tendall, London. 318 pp.

Robertson, O. H., and B. C. Wexler. 1962*a*. Histological changes in the pituitary gland of the rainbow trout (*Salmo gairdnerii*) accompanying sexual maturation and spawning. J. Morphol. 110: 157–169.

Robertson, O. H., and B. C. Wexler. 1962*b*. Histological changes in the pituitary gland of the Pacific salmon (genus *Oncorhynchus*) accompanying sexual maturation and spawning. J. Morphol. 110: 171–185.

Sathyanesan, A. G. 1963. Histological changes in the pituitary and their correlation with the gonadal cycle in some teleosts. Cellule 63: 283–290.

Sathyanesan, A. G. 1971. Structure of the hypothalamus of the freshwater teleost *Clarias batrachus* (L.). Z. Mikrosk. Anat. Forsch. (Leipz.) 84: 429–448.

Schreibman, M. P., J. F. Leatherland, and B. A. McKeown. 1973. Functional morphology of the teleost pituitary gland. Am. Zool. 13: 719–742.

Singh, T. P. 1971. Seasonal variations in the cyanophils and the gonadotropic potency of the pituitary in relation to gonadal activity in the catfish, *Mystus vittatus* (Bloch). Endokrinologie 56: 292–303.

Terlou, M., and B. Ekengren. 1979. Nucleus praeopticus and nucleus lateralis tuberis of *Salmo salar* and *Salmo gairdneri*: structure and relationship to the hypophysis. Cell Tissue Res. 197: 1–21.

Val-Sella, M. V., and F. Fava-De-Moraes. 1979. Morphology of the hypophysis of the freshwater teleost *Rhamdia hilarii* (Val., 1840). Anat. Anz. 145: 146–154.

van Oordt, P. G. W. J. 1965. Nomenclature of the hormone-producing cells in the adenohypophysis. Gen. Comp. Endocrinol. 5: 131–134.

van Overbeeke, A. P., and J. R. McBride. 1967. The pituitary gland of the sockeye (*Oncorhynchus nerka*) during sexual maturation and spawning. J. Fish. Res. Board Can. 24: 1791–1810.

van Overbeeke, A. P., and J. R. McBride. 1971. Histological effects of 11-ketotestosterone, 17-α-methyltestosterone, estradiol, estradiol cypionate, and cortisol on the interrenal tissue, thyroid gland, and pituitary gland of gonadectomized sockeye salmon (*Oncorhynchus nerka*). J. Fish. Res. Board Can. 28: 477–484.

Yoshie, S., and Y. Honma. 1978. Experimental demonstration of the cell types in the adenohypophysis of the gobiid fish, *Rhinogobius brunneus*. Arch. Histol. Jpn. 41: 129–140.

Thyroid Gland

Anderson, B. G., and D. L. Mitchum. 1974. Atlas of trout histology. Wyo. Game Fish Dep. Bull. 13. 110 pp.

Baker-Cohen, K. F. 1959. Renal and other heterotopic thyroid tissue in fishes. Pages 283–301 *in* A. Gorbman, ed. Comparative endocrinology. Wiley and Sons, New York.

Dodd, J. M., and A. J. Matty. 1964. Comparative aspects of thyroid function. Pages 303–356 *in* R. Pitt-Rivers and J. R. Tata, eds. The thyroid gland, vol. 1. Butterworth, London.

Gorbman, A. 1969. Thyroid function and its control in fishes. Pages 241–247 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

Fujita, H., H. Suemasa, and Y. Honma. 1967. An electron microscopic study of the thyroid gland of the silver eel, *Anguilla japonica* (a part of phylogenetic studies of the fine structure of the thyroid). Arch. Histol. Jpn. 27: 153–163.

Gardner, L. W., and H. E. Wachowski. 1960. Histological study of the thyroid and pituitary in the minnow *Gambusia* after exposure to high temperature and treatment with thiourea. Anat. Rec. 138: 365.

Gorbman, A., and H. S. Bern. 1962. A textbook of comparative endocrinology. Wiley and Sons Inc., New York. 468 pp.

Hoar, W. S. 1939. The thyroid gland of Atlantic salmon. J. Morphol. 65: 257–295.

Hoar, W. S. 1973. Comments on the evolution of thyroidal function in fish. Am. Zool. 13: 907–908.

Hoar, W. S. and G. M. Bell. 1950. The thyroid gland in relation to the seaward migration of Pacific salmon. Can. J. Res., Sect. D., Zool. Sci. 28: 126–136.

Olivereau, M. 1958. Anatomical and histological study of the thyroid gland of the tuna. Bull. Soc. Zool. France 82: 401–417.

Sage, M. 1973. The evolution of thyroidal function in fishes. Am. Zool. 13: 899–905.

Swift, D. R. 1960. Cyclical activity of the thyroid gland of fish in relation to environmental changes. Symp. Zool. Soc. Lond. 2: 17–27.

Adrenal Gland

Butler, D. G. 1973. Structure and function of the adrenal gland of fishes. Am. Zool. 13: 839–879.

Chavin, W. 1906. Adrenal histochemistry of some freshwater and marine teleosts. Gen. Comp. Endocrinol. 6: 183–194.

Grynszpan-Winograd, O. 1975. Ultrastructure of the chromaffin cell. Pages 295–308 *in* Handbook of physiology, vol. 6. American Physiological Society, Washington.

Gupta, O. P., and R. K. Shrivastava. 1971. Morphological studies of the interrenal bodies, mesonephric kidneys and the urinary bladder of the Indian gar-pike, *Xenentodon cancila* (Ham.). Okajimas Folia Anat. Jpn. 48: 205–211.

Hanke, W. 1967. Histological and physiological evidence for the regulation of the adrenal cortex by the pituitary in poikilotherm vertebrates. Pages 1073–1083 *in* Proceedings of the 2nd International Congress on Hormonal Steroids. Excerpta Med. Int. Congr. Ser. No. 132.

Hanke, W., and I. C. Jones. 1966. Histological and histochemical studies on the adrenal cortex and the corpuscles of Stannius of the European eel *Anguilla anguilla* L. Gen. Comp. Endocrinol. 7: 166–178.

Hadisty, M. W., and M. Baines. 1971. The ultrastructure of the interrenal tissue of the lamprey. Experientia (Basel) 27: 1072–1075.

Hill, C. W., and P. O. Fromm. 1968. Response of the interrenal gland of rainbow trout (*Salmo gairdnerii*) to stress. Gen. Comp. Endocrinol. 11: 69–77.

Hillarp, N.-A., and B. Hokfelt. 1955. Histochemical demonstration of noradrenoline and adrenaline in the adrenal medulla. J. Histochem. Cytochem. 3: 1–5.

Honma, Y. 1960. Studies on the endocrine glands of the salmonoid fish, ayu, *Plecoglossus altivelis* Temminck et Schlegel. III. Changes in the adrenal cortical tissues during the life-span of the fish. Annot. Zool. Jpn. 33: 234–240.

Hooli, M. A., and V. B. Nadkarni. 1975. Functional morphology of the interrenal and chromaffin cells in the teleosts, *Rasbora daniconius*, *Barbus stigma* and *Channa gachu*. Acta Anat. 93: 367–375.

Hooli, M. A., and V. B. Nadkarni. 1976. A histological and histochemical study of interrenal gland in two teleosts, *Cirrhina mrigala* and *Labeo rohita*. J. Anim. Morphol. Physiol. 23: 199–204.

Idler, D. R. 1973. Comments on "Structure and function of the adrenal gland of fishes" by David Gordon Butler. Am. Zool. 13: 881–884.

Jung, B., M. E. Moritz, and J. P. Berchtold. 1981. Fine structure and function of interrenal (adrenocortical) cells of dexamethasone-treated trout (*Salmo fario* L.). Cell Tissue Res. 214: 641–649.

Mahon, E. F., W. S. Hoar, and S. Tabata. 1962. Histophysiological studies on the adrenal tissues of the goldfish. Can. J. Zool. 40: 449–464.

McBride, J. R., and A. P. van Overbeeke. 1969. Hypertrophy of the interrenal tissue in sexually maturing sockeye salmon (*Oncorhynchus nerka*) and the effect of gonadectomy. J. Fish. Res. Board Can. 26: 2975–2985.

McMillan, P. J., W. M. Hooker, B. A. Roos, and L. J. Deftos. 1976. Ultimobranchial gland of the trout (*Salmo gairdneri*). Gen. Comp. Endocrinol. 28: 313–319.

Nandi, J. 1962. The structure of the interrenal gland in teleost fishes. Univ. Calif. Publ. Zool. 65: 129–212.

Oguri, M. 1960*a*. Studies on the adrenal glands of teleosts. III. On the distribution of chromaffin cells and interrenal cells in the head kidneys of fishes. Bull. Jpn. Soc. Sci. Fish. 26: 443–447.

Oguri, M. 1960*b*. Studies on the adrenal glands of teleosts. IV. Histochemistry of the interrenal cells of fishes. Bull. Jpn. Soc. Sci. Fish. 26: 448–451.

Oguri, M. 1960*c*. Some histological observations on the interrenal bodies of elasmobranchs. Bull. Jpn. Soc. Sci. Fish. 26: 481–485.

Olivereau, M., and M. Froentin. 1954. The effect of hypophysectomy on the histology of the anterior interrenal tissue in the eel, *Anguilla anguilla*. Ann. Endocrinol. 15: 805–826.

Olivereau, M., and J. Olivereau. 1970. Effect of prolactin in intact and hypophysectomized eels. VI. Histological structure of interrenal and water and electrolyte metabolism. Z. Vgl. Physiol. 68: 429–445.

Piezzi, R. S. 1965. Two types of chromaffin cells in the adrenal gland of the "*Bufo arenarum*" Hensel. Acta Physiol. Lat. Am. 15: 96–100.

Robertson, O. H., and B. C. Wexler. 1959. Hyperplasia of the adrenal cortical tissue in Pacific salmon (genus *Oncorhynchus*) and rainbow trout (*Salmo gairdnerii*) accompanying sexual maturation and spawning. Endocrinology 65: 225–238.

Thakur, D. P. 1975. Histochemical observations on the adrenal tissue of the teleost fish, *Nandus*. Folia Morphol. (Prague) 23: 65–70.

Yamamoto, K., and H. Onozato. 1965. The fine structure of the interrenal tissue of the goldfish. Anat. Zool. Jpn. 38: 140–150.

Yaron, Z. 1970. The chromaffin and interrenal cells of *Acanthobrama terraesanctae* (Cyprinidae, Teleostei). Gen. Comp. Endocrinol. 14: 542–550.

Yoakim, E. G., and J. M. Grizzle. 1980. Histological, histochemical and ultrastructural studies on the interrenal and chromaffin cells of the fathead minnow, *Pimephales promelas* Rafinesque. J. Fish Biol. 17: 477–494.

Youson, J. H., D. G. Butler, and A. T. C. Chan. 1975. Identification and distribution of the adrenocortical homolog, chromaffin tissue and corpuscles of Stannius in *Amia calva* L. Gen. Comp. Endocrinol. 29: 198–211.

Corpuscles of Stannius

Anderson, B. G., and D. L. Mitchum. 1974. Atlas of trout histology. Wyo. Game Fish Dep. Bull. 13. 110 pp.

Belsare, D. 1973. Comparative anatomy and histology of the corpuscles of Stannius in teleosts. Z. Mikrosk. Anat. Forsch. (Leipz.) 87: 445–456.

Bhattacharyya, T. K., D. G. Butler, and J. H. Youson. 1982. Ultrastructure of the corpuscles of Stannius in the garpike (*Lepisosteus platyrhynchus*). Gen. Comp. Endocrinol. 46: 29–41.

Butler, D. G. 1969. Corpuscles of Stannius and renal physiology in the eel (*Anguilla rostrata*). J. Fish. Res. Board Can. 26: 639–654.

Carpenter, S. J., and H. L. Heyl. 1974. Fine structure of the corpuscles of Stannius of Atlantic salmon during the freshwater spawning journey. Gen. Comp. Endocrinol. 23: 212–223.

Chan, D. K. O. 1972. Hormonal regulation of calcium balance in teleost fish. Gen. Comp. Endocrinol. Suppl. 3: 411–420.

Chester Jones, I., D. K. O. Chan, I. W. Henderson, and J. N. Ball. 1969. The adrenocortical steroids, adrenocorticotropin and the corpuscles of Stannius. Pages 321–376 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

Cohen, R. S., P. K. T. Pang, and N. B. Clark. 1975. Ultrastructure of the Stannius corpuscles of the killifish *Fundulus heteroclitus*, and its relation to calcium regulation. Gen. Comp. Endocrinol. 27: 413–423.

Fenwick, J. C. 1974. The corpuscles of Stannius and calcium regulation in the North American eel (*Anguilla rostrata* LeSueur). Gen. Comp. Endocrinol. 23: 127–135.

Fujita, J., and Y. Honma. 1967. On the fine structure of the corpuscles of Stannius of the eel, *Anguilla japonica*. Z. Zellforsch. Mikrosk. Anat. 77: 175–187.

Hanke, W., K. Bergerhoff, and D. K. O. Chan. 1967. Histological observations on pituitary ACTH-cells, adrenal cortex and the corpuscles of Stannius of the European eel (*Anguilla anguilla* L.). Gen. Comp. Endocrinol. 9. 64–75.

Heyl, H. L. 1970. Changes in the corpuscles of Stannius during the spawning journey of Atlantic salmon (*Salmo salar*). Gen. Comp. Endocrinol. 14: 43–52.

Hoshiai, G., Y. Sugawara, and R. Sato. 1970. Structure of Stannius corpuscles in the chum salmon, *Oncorhynchus keta* (Walbaum), with special reference to morphological changes during growth. Med. Biol. (Helsinki). 80: 1-6.

Johnson, D. W. 1972. Variations in the interrenal and corpuscles of Stannius of *Mugil cephalus* from the Colorado River and its estuary. Gen. Comp. Endocrinol. 19: 7–25.

Krishnamurthy, V. G., and H. A. Bern. 1969. Correlative histologic study of the corpuscles of Stannius and the juxtaglomerular cells of teleost fishes. Gen. Comp. Endocrinol. 13: 313–335.

Krishnamurthy, V. G., and H. A. Bern. 1971. Innervation corpuscles of Stannius. Gen. Comp. Endocrinol. 16: 162–165.

Lopez, E. 1969. Etude histophysiologique des corpuscles de Stannius de *Salmo salar* L. au cours des diverses etapes de son cycle vital. Gen. Comp. Endocrinol. 12: 339–349.

Meats, M., P. M. Ingleton, I. C. Jones, H. O. Garland, and C. J. Kenyon. 1979. Fine structure of the corpuscles of Stannius of the trout *Salmo gairdneri*: structural changes in response to increased environmental salinity and calcium ions. Gen. Comp. Endocrinol. 36: 451–461.

Mezhnin, F. I. 1979. Stannius corpuscles in fish. J. Ichthyol. 9: 105–123. [Engl. Transl. Vopr. Ikhtiol.]

Ogawa, M. 1967. Fine structure of the corpuscles of Stannius and the interrenal tissue in goldfish, *Carassius auratus*. Z. Zellforsch. Mikrosk. Anat. 81: 174–189.

Oguri, M. 1966. Electron-microscopic observations on the corpuscles of Stannius in goldfish. Bull. Jpn. Soc. Sci. Fish. 32: 902–908.

Oguri, M., and H. Sokabe. 1974. Comparative histology of the corpuscles of Stannius and the juxtaglomerular cells in the kidneys of teleosts. Bull. Jpn. Soc. Sci. Fish. 40: 545–549.

Pang, P. K. T. 1971. The relationship between corpuscles of Stannius and serum electrolyte regulation in killifish, *Fundulus heteroclitus*. J. Exp. Zool. 178: 1–8.

Pang, P. K. T. 1973. Endocrine control of calcium metabolism in teleosts. Am. Zool. 13: 775–792.

Pang, P. K. T., and R. K. Pang. 1974. Environmental calcium and hypocalcium activity in the Stannius corpuscles of the channel catfish, *Ictalurus punctatus* (Rafinesque). Gen. Comp. Endocrinol. 23: 239–241.

Pang, P. K. T., R. K. Pang, and W. H. Sawyer. 1973. Effects of environmental calcium and replacement therapy on the killifish, *Fundulus heteroclitus*, after the surgical removal of the corpuscles of Stannius. Endocrinology 93: 705–710.

Rasquin, P. 1956. Cytological evidence for a rôle of the corpuscles of Stannius in the osmoregulation of teleosts. Biol. Bull. (Woods Hole) 111: 399–409.

Schreibman, M. P., and P. K. T. Pang. 1975. The histophysiology of transplanted corpuscles of Stannius in the killifish *Fundulus heteroclitus*. Gen. Comp. Endocrinol. 26: 186–191.

Tomasulo, J. A., W. D. Belt, and E. R. Hayes. 1970. The fine structure of the Stannius body of the guppy and its response to deionized water. Am. J. Anat. 129: 307–328.

Unsicker, K., T. Polonius, R. Lindmar, K. Loffelholz, and U. Wolf. 1977. Catechloamines and 5-hydroxytryptamine in corpuscles of Stannius of the salmonid, *Salmo irideus* L. A study correlating electron microscopical, histochemical and chemical findings. Gen. Comp. Endocrinol. 31: 121–132.

Wendelaar Bonga, S. E., and J. A. Greven. 1975. A second cell type in Stannius bodies of two euryhaline teleost species. Cell Tissue Res. 159: 287–290.

Wendelaar Bonga, S. E., J. A. Greven, and M. Veenhuis. 1977. Vascularization, innervation and ultrastructure of the endocrine cell types of Stannius corpuscles in the teleost, *Gasterosteus aculeatus*. J. Morphol. 153: 225–244.

Wendelaar Bonga, S. E., J. C. A. van der Meij, and P. K. T. Pang. 1980. Evidence for two secretory cell types in the Stannius bodies of the teleosts *Fundulus heteroclitus* and *Carassius auratus*. Cell Tissue Res. 212: 295–306.

Youson, J. H., and D. G. Butler. 1976. Fine structure of the adrenocortical homologue and the corpuscles of Stannius of *Amia calva* L. Acta Zool. (Stockh.) 57: 217–230.

Youson, J. H., D. G. Butler, and A. T. C. Chan. 1976. Identification and distribution of the adrenocortical homolog, chromaffin tissue, and corpuscles of Stannius in *Amia calva* L. Gen. Comp. Endocrinol. 29: 198–211.

Saccus Vasculosus

Emanuelsson, H., and C. von Mecklenburg. 1972. Metabolic activity in the saccus vasculosus of the rainbow trout, *Salmo gairdneri* (Richardson). Z. Zellforsch. Mikrosk. Anat. 130: 351–361.

Emanuelsson, H., and C. von Mecklenburg. 1974. Experimental and structural analysis of the function of saccus vasculosus in rainbow trout, *Salmo gairdneri* (Richardson). Cell Tissue Res. 148: 27–44.

Galer, B. B., and D. C. Billenstien. 1972. Ultrastructural development of the saccus vasculosus in rainbow trout (*Salmo gairdneri*). Z. Zellforsch. Mikrosk. Anat. 128: 162–174.

Jansen, W. F. 1975. The saccus vasculosus of the rainbow trout, *Salmo gairdneri* Richardson. A cytochemical and enzyme-cytochemical study, particularly with respect to coronet cells and glial cells. Neth. J. Zool. 25: 309–331.

Jansen, W. F., E. H. Burger, and H. A. Zandbergen. 1982. Subcellular localization of calcium in the coronet cells and tanycytes of the saccus vasculosis of the rainbow trout, *Salmo gairdneri* Richardson. Cell Tissue Res. 224: 169–180.

Jansen, W. F., and W. F. G. Flight. 1969. Light and electronmicroscopical observations on the saccus vasculosus of the rainbow trout. Z. Zellforsch. Mikrosk. Anat. 100: 439–465.

Jansen, W. F., and J. B. van Dort. 1978. Further investigations on the structure and function of the saccus vasculosus of the rainbow trout, *Salmo gairdneri* Richardson. Ultrastructural cytochemistry of membrane-bound alkaline phosphatase. Cell Tissue Res. 187: 61–68.

Joy, K. P., and A. G. Sathyanesan. 1979. A histoenzymological study of the saccus vasculosus of the freshwater teleost, *Clarias batrachus* (L.). Z. Mikrosk. Anat. Forsch. (Leipz.) 93: 297–304.

Katagishi, M. 1961. Histological observation on the saccus vasculosus of fishes. Arch. Histol. Jpn. 21: 369–385.

Kurotaki, M. 1961. The submicroscopic structure of the epithelium of saccus vasculosus in two teleosts. Acta Anat. Nippon. 36: 277–288.

Lanzing, W. J. R., and E. W. Van Lennep. 1970. Ultrastructure of the saccus vasculosus of teleost fishes. I. The coronet cell. Aust. J. Zool. 18: 353–371.

Murakami, M., and T. Yoshida. 1967. Elektronenmikroskopische Beobachtungen am Saccus vasculosus des Kugelfishes, *Spheroides niphobles*. Arch. Histol. Jpn. 28: 265–284.

Sundararaj, B. I., and M. R. N. Prasad. 1963. Role of saccus vasculosus in teleosts—a new interpretation. Naturwissenschaften 50: 362–363.

van de Kamer, J. C., J. Boddingius, and J. Boender. 1960. On the structure and function of the saccus vasculosus of the rainbow trout (*Salmo irideus*). Z. Zellforsch. Mikrosk. Anat. 52: 494–500.

von Mecklenburg, C. 1973. Ultrastructural changes in the coronet cells of the saccus vasculosus from rainbow trout, *Salmo gairdneri* (Richardson), kept in sea water. Z. Zellforsch. Mikrosk. Anat. 139: 271–284.

von Mecklenburg, C. 1974. The development of saccus vasculosus in two teleosts. Acta Zool. 55: 137–148.

Watanabe, A. 1966. Light and electron microscope studies on the saccus vasculosus of the ray (*Danyatis akajei*). Arch. Histol. Jpn. 27: 427–449.

Zimmerman, H. 1972. Ultrastrukturelle und cytochemische Untersuchungen am Saccus vasculosus von Knochenfischen unter besonderer Berucksichtigung der Innervation. Z. Zellforsch. Mikrosk. Anat. 128: 240–260.

Ultimobranchial Glands

Copp, D. H. 1969. The ultimobranchial glands and calcium regulation. Pages 277–398 *in* W. S. Hoar and D. J. Randall, eds. Fish physiology, vol. 2. Academic Press, New York.

McMillan, P. J., W. M. Hooker, B. A. Roos, and L. J. Deftos. 1976. Ultimobranchial gland of the trout (*Salmo gairdneri*). I. Immunohistology and radioimmunoassay of calcitonin. Gen. Comp. Endocrinol. 28: 313–319.

Oguri, M. 1973. Seasonal histologic changes in the ultimobranchial gland of goldfish. Bull. Jpn. Soc. Sci. Fish. 39: 851–858.

Pang, P. K. T. 1971. Calcitonin and ultimobranchial glands in fishes. J. Exp. Zool. 178: 89–100.

Robertson, D. R. 1969. Some morphological observations of the ultimobranchial gland in the rainbow trout, *Salmo gairdneri*. J. Anat. 105: 115–1[illegible]7.

Tan-Tue, V. 1970. Histology of the ultimobranchial bodies of *Chimaera monstrosa*. Arch. Anat. Microsc. Morphol. Exp. 59: 21–36.

Yamane, S. 1981. Sexual difference of ultrastructure of the ultimobranchial gland of mature eels (*Anguilla japonica*). Bull. Fac. Fish. Hokkaido Univ. 32: 1–5.

Yamane, S., and J. Yamada. 1977. Histological changes of the ultimobranchial gland through the life history of the Masu salmon. Bull. Jpn. Soc. Sci. Fish. 43: 375–386.

Plate 53. Pituitary Gland (1)

Fig. 1. Section of the brain of a sexually immature 10-month-old rainbow trout, showing both the pituitary and the saccus vasculosus. × 40.

- a. Saccus vasculosus
- b. Pars intermedia
- c. Rostral pars distalis
- d. Neurohypophysis
- e. Stalk of the hypophysis
- f. Infundibulum

Fig. 2. Section of the anterior lobe of the pituitary. × 400.

- a. Follicle in the rostral pars distalis
- b. Lumen of follicle
- c. Neurohypophysis

Fig. 3. Detail of the pituitary gland at point of contact with the saccus vasculosus. × 400.

- a. Saccus vasculosus
- b. Neurohypophysis
- c. Pars intermedia
- d. Pars distalis

a
e
d
b
c
1

a
b
c
2

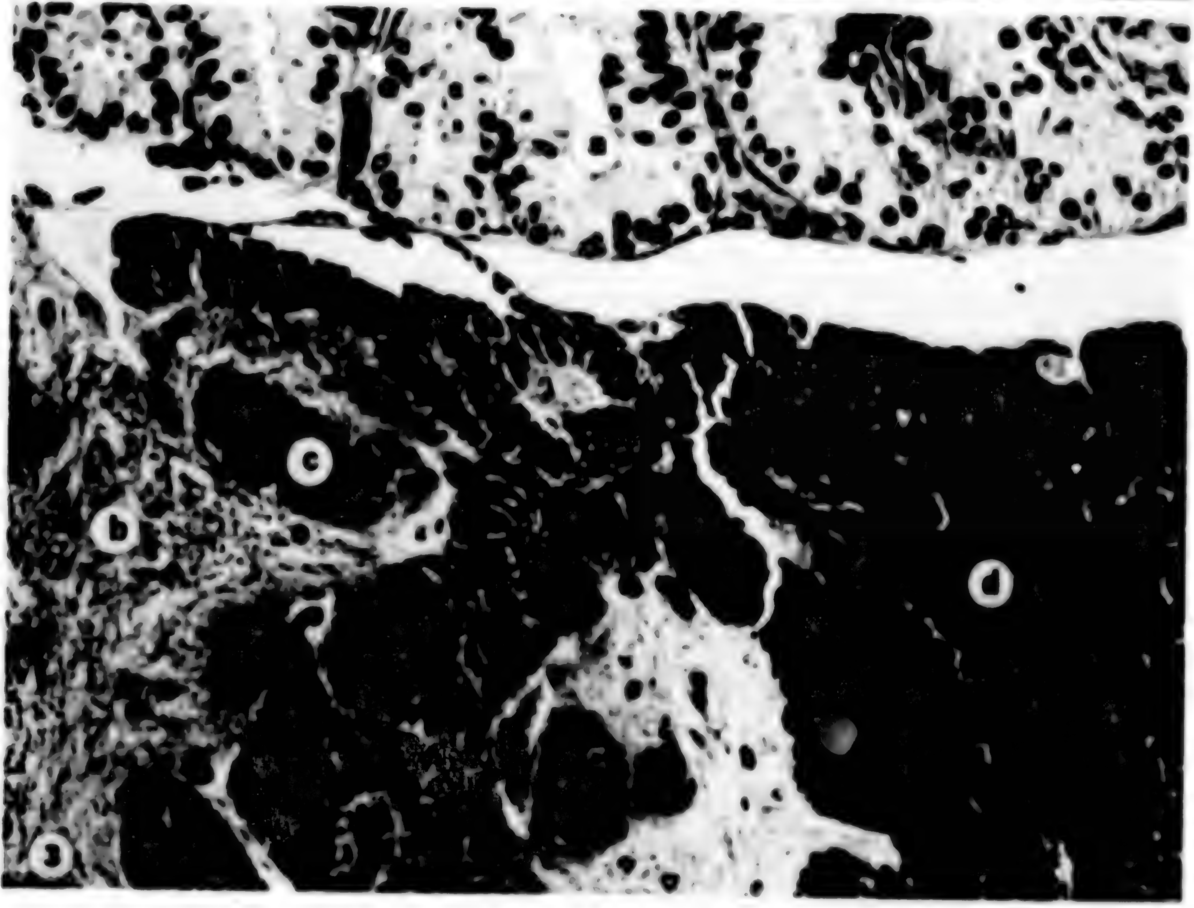

c
b
d
3

Plate 54. Pituitary (2)

Fig. 1. Sagittal section of the pituitary gland area of a sexually immature 10-month-old rainbow trout. Masson's trichrome stain. × 140.

- a. Diencephalon
- b. Infundibulum
- c. Neurohypophysis
- d. Rostral pars distalis
- e. Proximal pars distalis
- f. Pars intermedia
- g. Saccus vasculosus

Fig. 2. Detail of rostral pars distalis of Fig. 1. × 460.

- a. Neurohypophysis
- b. Prolactin cells forming follicles
- c. Corticotrophs or adrenocorticotropic (ACTH) cells

Fig. 3. Detail of rostral pars distalis and proximal pars distalis of Fig. 1. × 475.

- a. Neurohypophysis
- b. Somatotrophs, somatotropin hormone producing cells
- c. Corticotrophs or adrenocorticotropic (ACTH) cells
- d. Prolactin cells

a
a
1

a
2

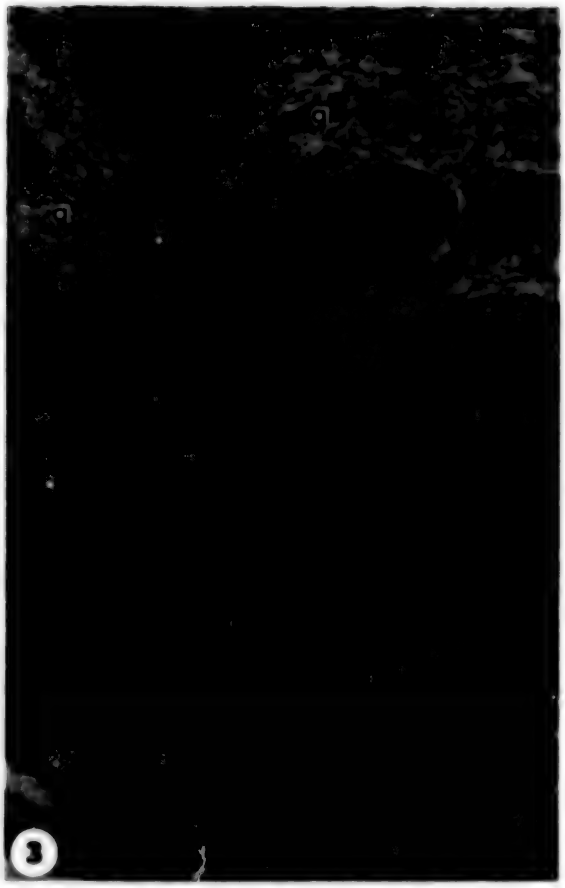

a
a
3

Plate 55. Pituitary (3)

Sagittal section of the rostral pars distalis and proximal pars distalis regions of a 14-month-old rainbow trout. Periodic acid Schiff (PAS)-orange G-light green stain. × 440.

a. Somatotrophs. These somatotropin hormone producing cells are orange G positive.
b. Thyrotrophs or gonadotrophs. These PAS positive cells could be either thyroid stimulating hormone or gonadotropin hormone producing cells.
c. Corticotrophs. Light green positive adrenocorticotrophic (ACTH) cells.
d. Prolactin cells. These cells are PAS negative.

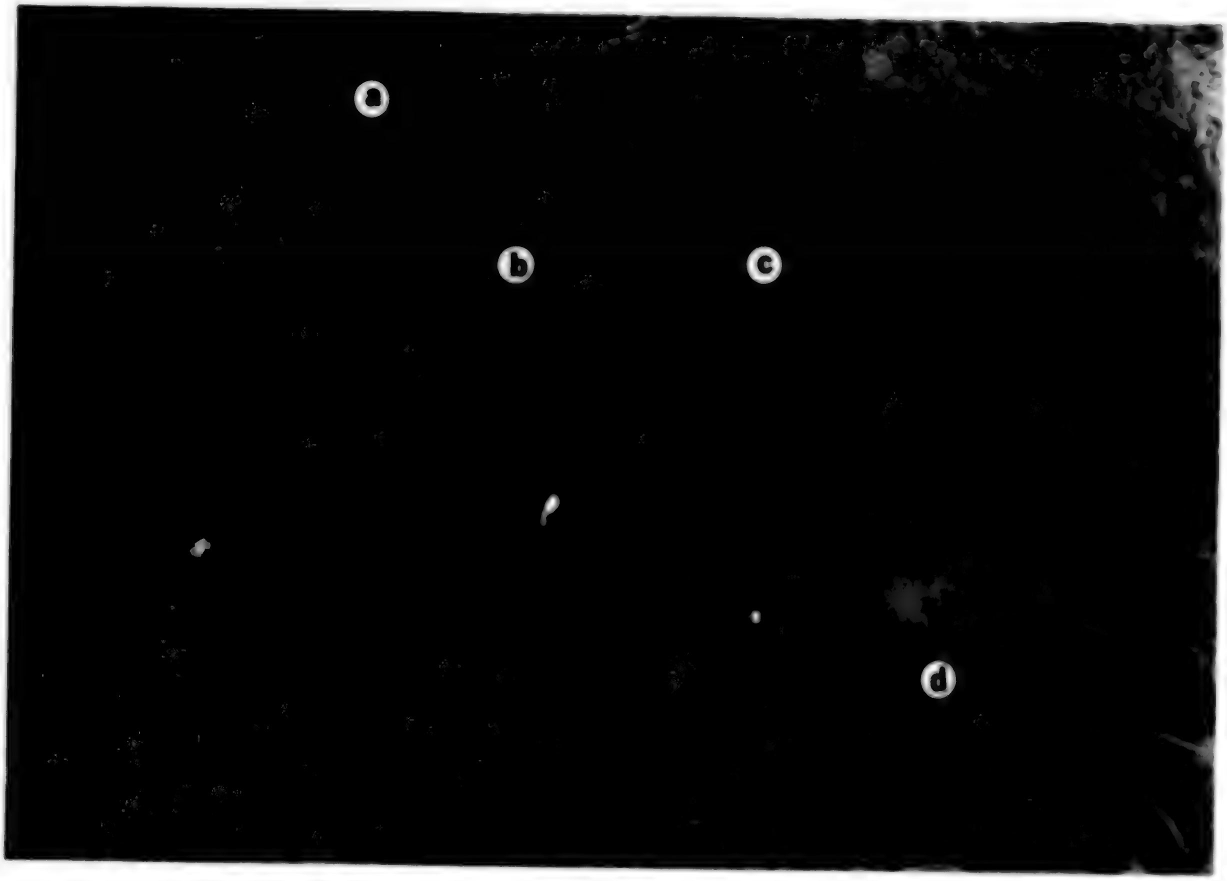

a
b
c
d

Plate 56. Thyroid Gland

Fig. 1. Cross section of head of 3-month-old rainbow trout. × 50.

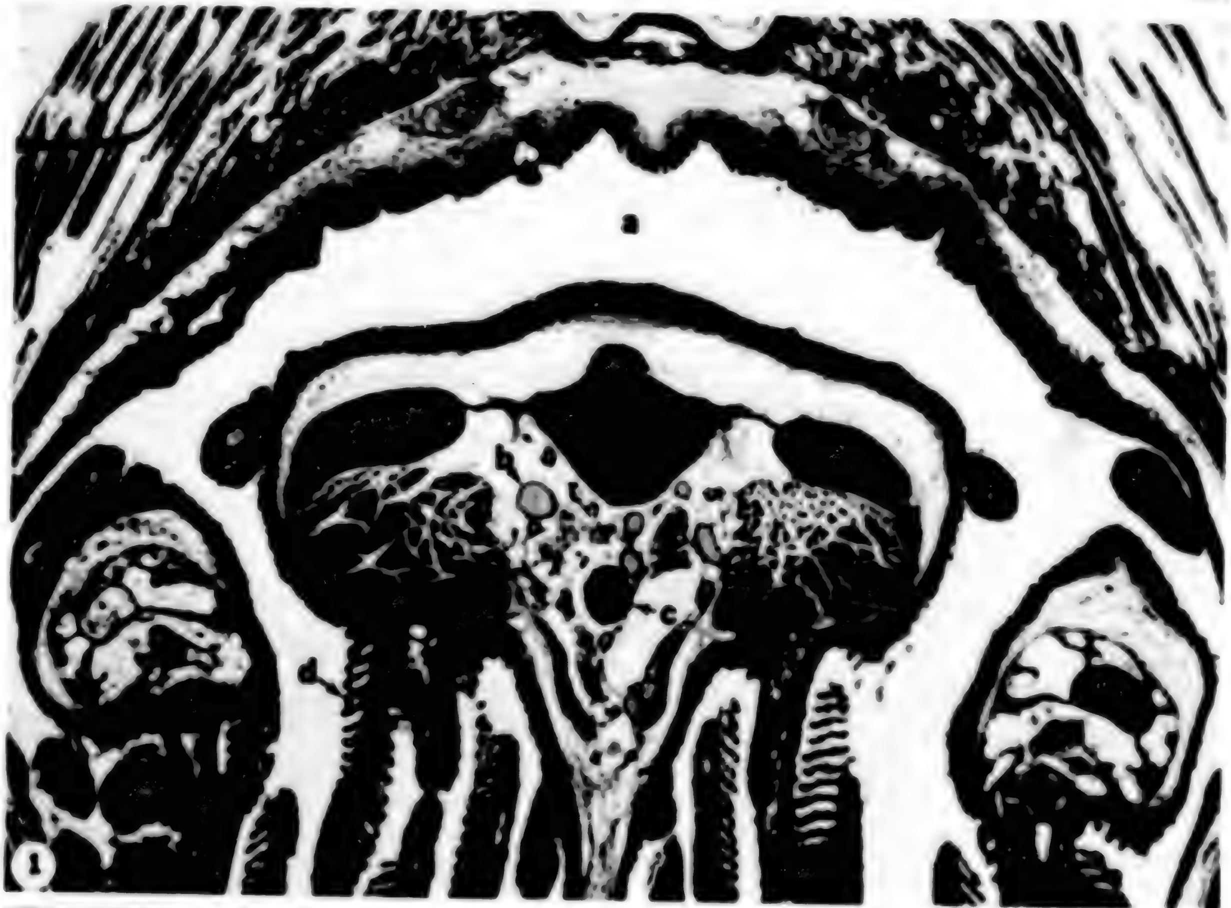
- a. Buccal cavity
- b. Follicle of the thyroid gland
- c. Aorta
- d. Gill filament

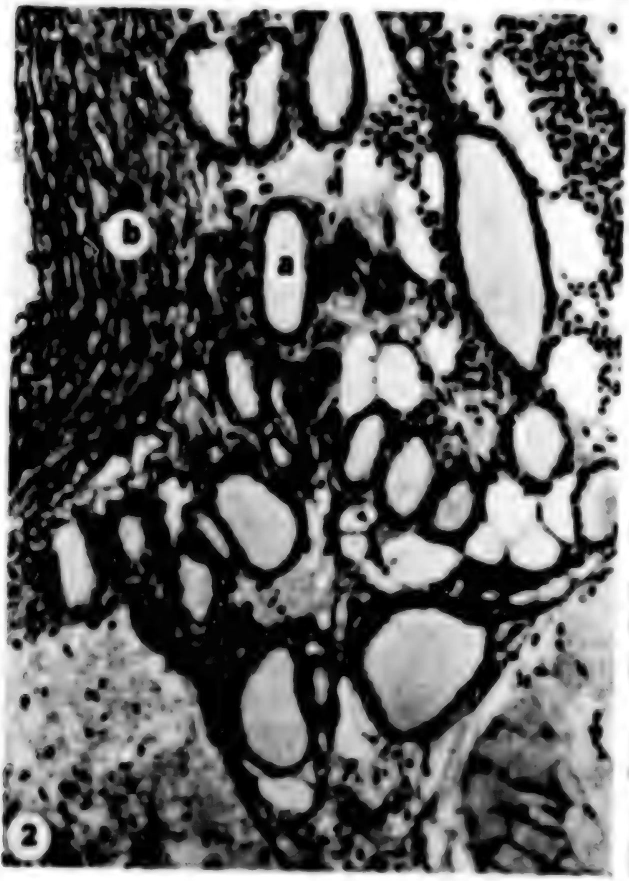
Fig. 2. Detail of the thyroid gland. × 200.

- a. Thyroid follicle
- b. Wall of the aorta

Fig. 3. Detail of thyroid follicles. × 450.

- a. Nucleus of follicle cell
- b. Colloid
- c. Vacuole


a
b
c
d
1


b
a
2

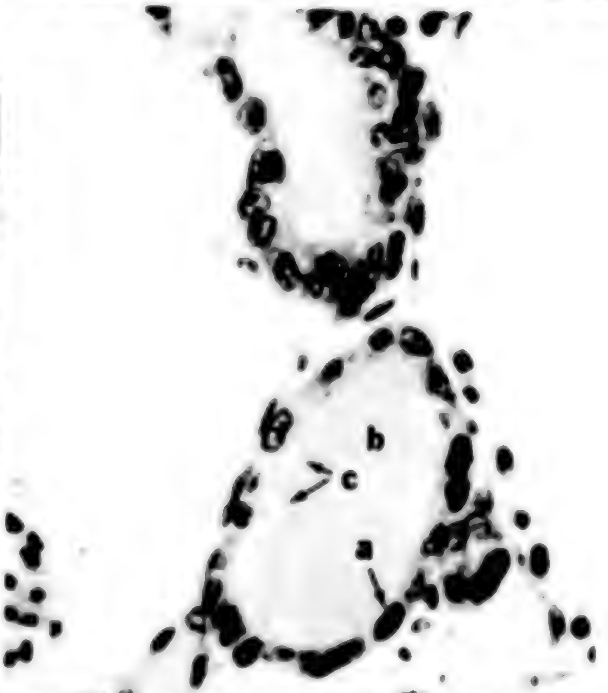

b
c
a
3

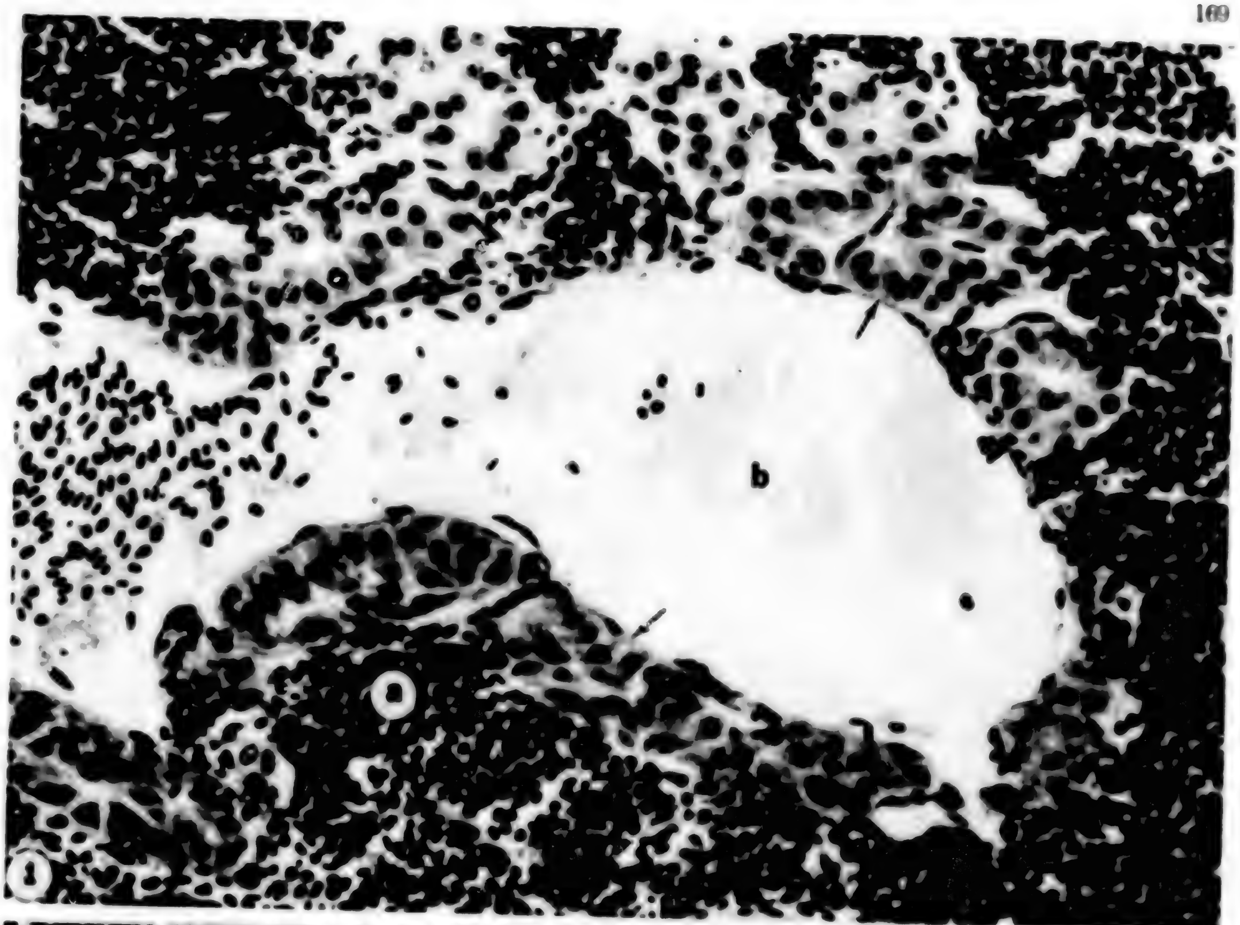
Plate 57. Adrenal Glands

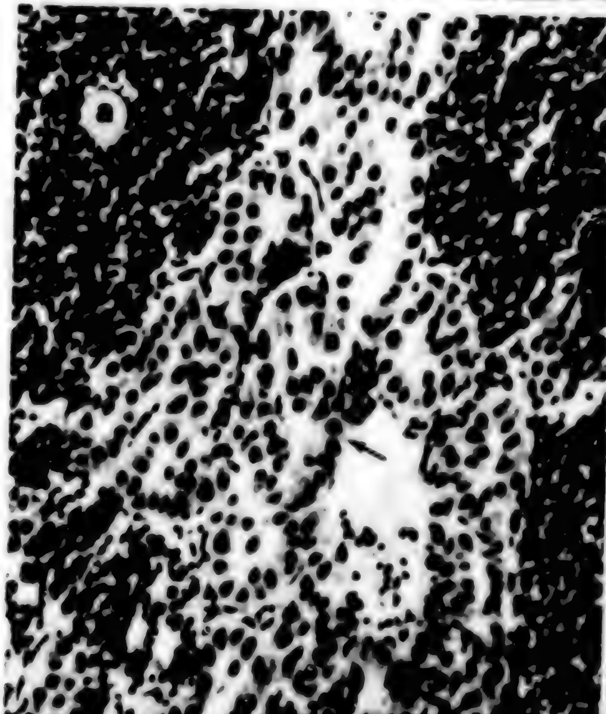
Fig. 1. Section of the hematopoietic head kidney of a yearling rainbow trout, showing interrenal tissue (arrows) lying adjacent to the ramifications of the postcardinal veins. The characteristic features of these endocrine cells are pale cytoplasm and dark, contrasting nuclei. × 320.

a. Hematopoietic tissue of the head kidney
b. Postcardinal vein

Fig. 2. Different section of the kidney shown in Fig. 1. The interrenal tissue (arrow) is usually associated with the blood vessels, although islets are occasionally scattered through the hematopoietic tissue. × 320.

Fig. 3. Chromaffin cells (arrows) lining a cardinal vein of the trout head kidney. × 725.


b
1


2

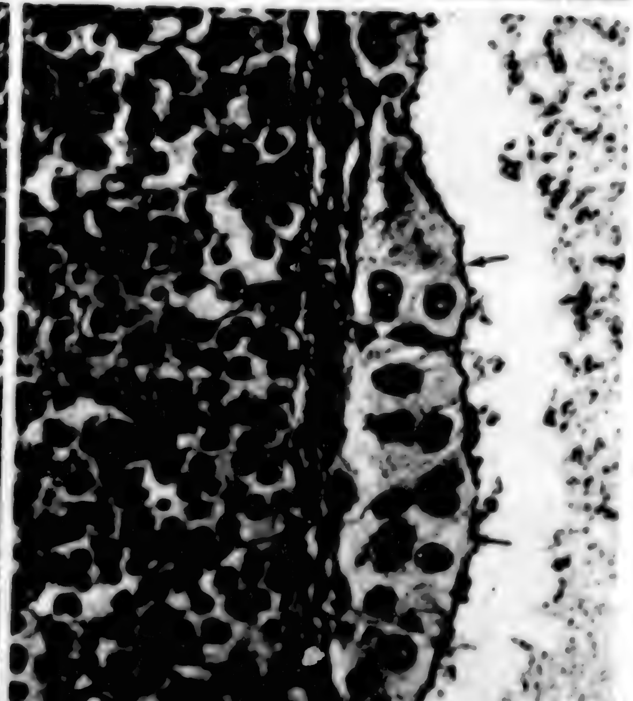

3

Plate 58. Chromaffin cells

Section of the postcardinal vein area from the head kidney of a 14-month-old rainbow trout. Stained by the potassium dichromate-chromate method. × 540.

a. Interrenal cells
b. Chromaffin cells. Note slightly brown chromate positive cells. Nuclei of these cells also appear to have chromatin margination with somewhat clear cytoplasm.
c. Hematopoietic tissue of the head kidney
d. Postcardinal vein

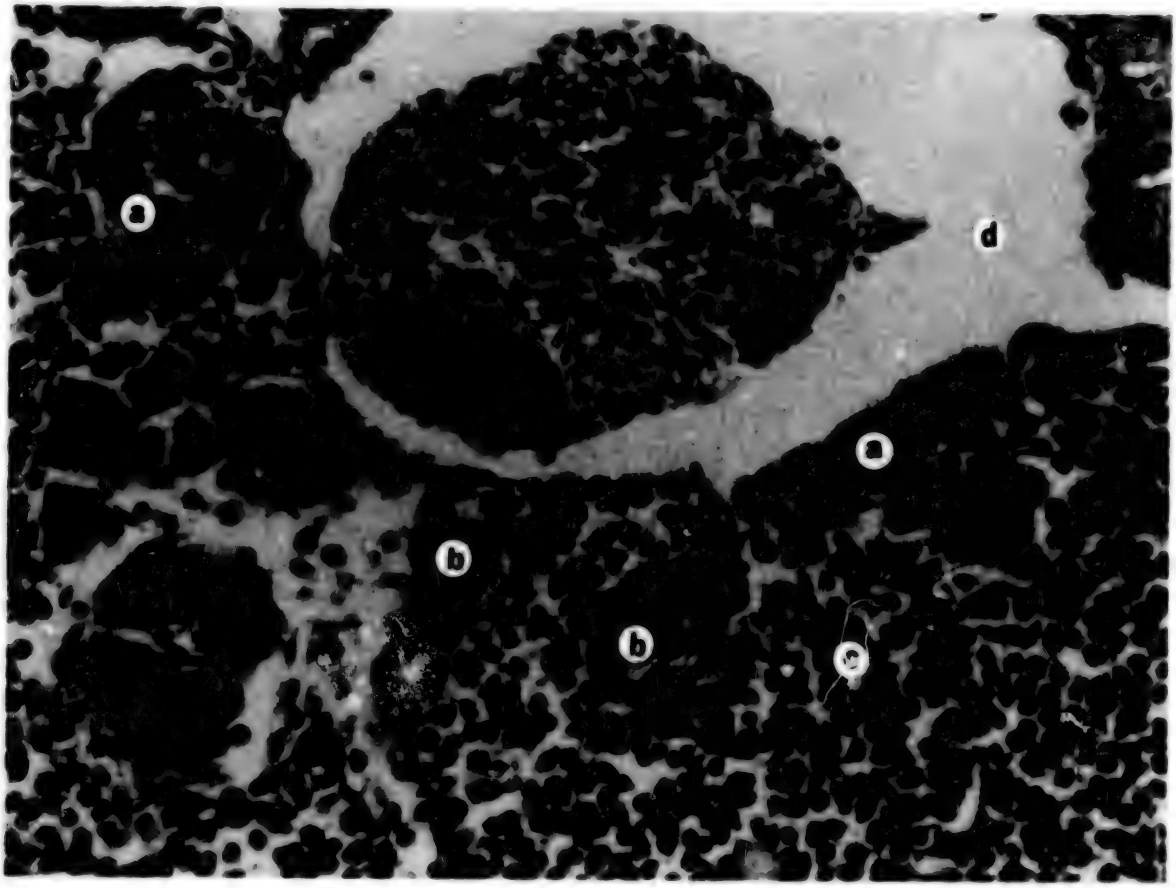

a
d
a
b
b
c

Plate 59. Corpuscle of Stannius (1)

Fig. 1. Section through the excretory kidney of young-of-the-year rainbow trout, showing a large, oval corpuscle of Stannius. × 40.

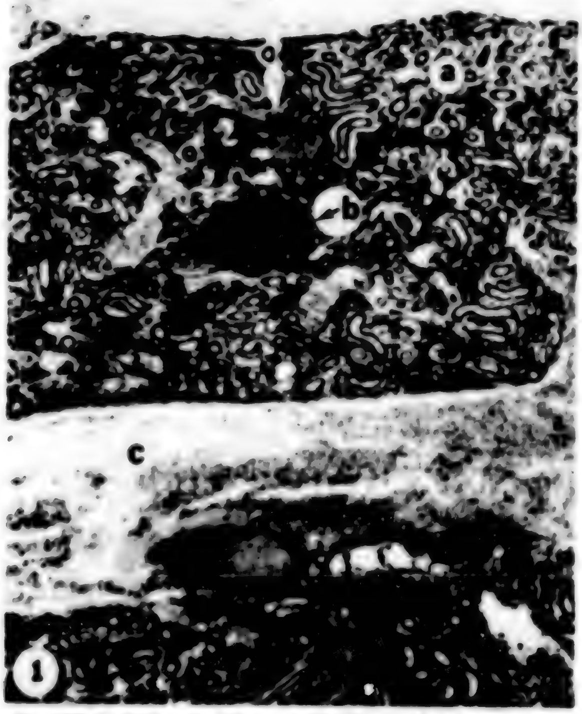
a. Renal kidney
b. Corpuscle of Stannius
c. Blood vessel

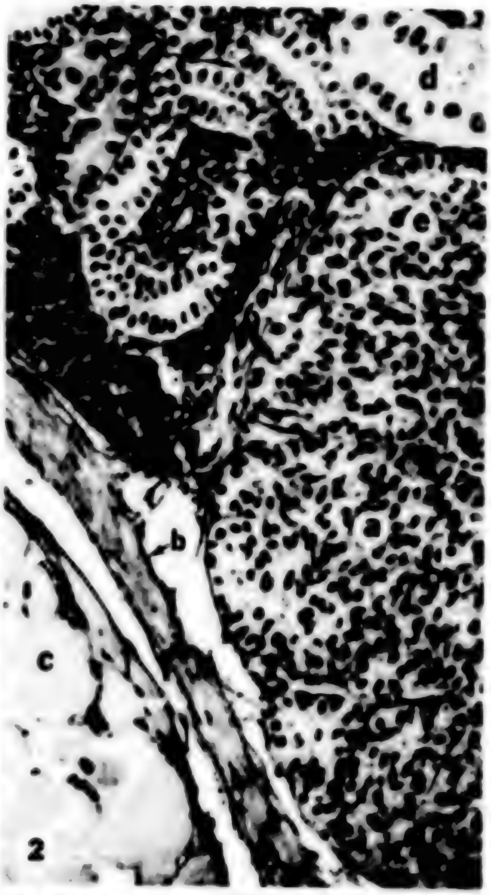
Fig. 2. Detail of corpuscle of Stannius lying adjacent to the lateral body musculature. × 250.

a. Corpuscle of Stannius
b. Capsule or urinary sheath
c. Lateral musculature
d. Renal tubule

Fig. 3. Corpuscle of Stannius shown in Fig. 1. × 250.

a. Hematopoietic tissue of the kidney
b. Renal capillary with erythrocytes
c. Tangential section of a renal tubule
d. Corpuscle of Stannius composed of many lobules


a
b
c
1


d
e
a
b
c
2

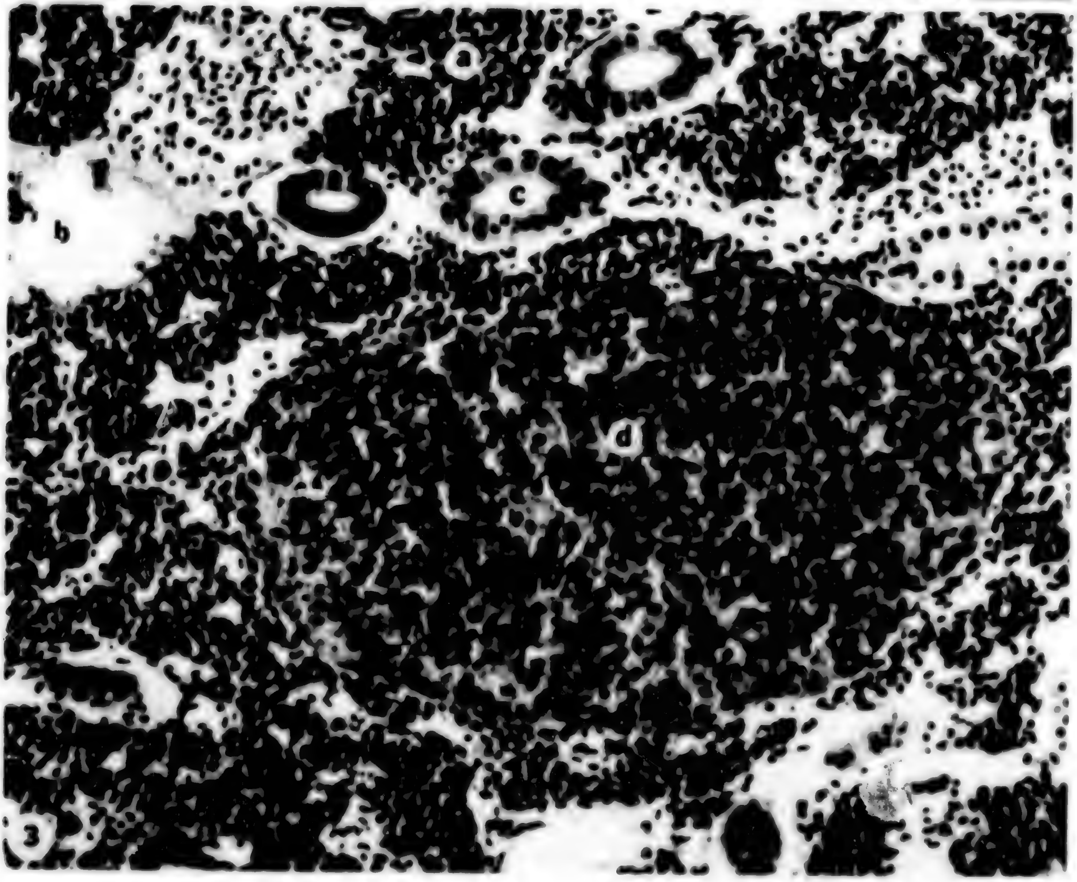

a
b
c
d
3

Plate 60. Corpuscle of Stannius (2)

Section of the mid-kidney of a 12-month-old rainbow trout. May-Grunwald Giemsa stain. × 1600.

a. Hematopoietic tissue
b. Renal tubule
c. Corpuscle of Stannius
d. Melanophores

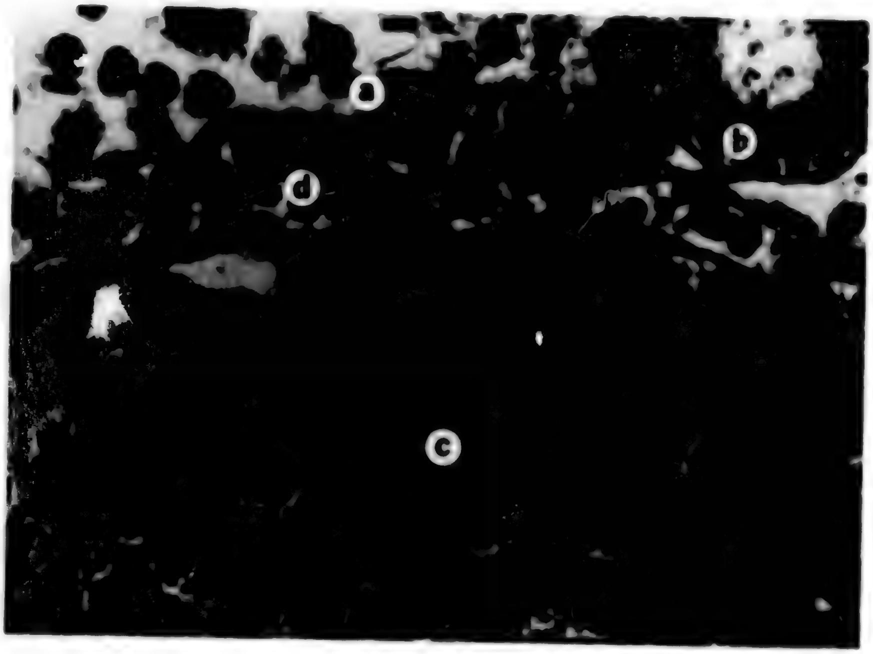

a
b
d
c

Plate 61. Saccus Vasculosus

Fig. 1. Cross section of the head of a 3-month-old rainbow trout. × 40.

- a. Optic lobe
- b. Inferior lobe
- c. Saccus vasculosus

Fig. 2. Higher magnification of Fig. 1c showing the characteristic folded structure and the blood vessels lying within the folds. × 250.

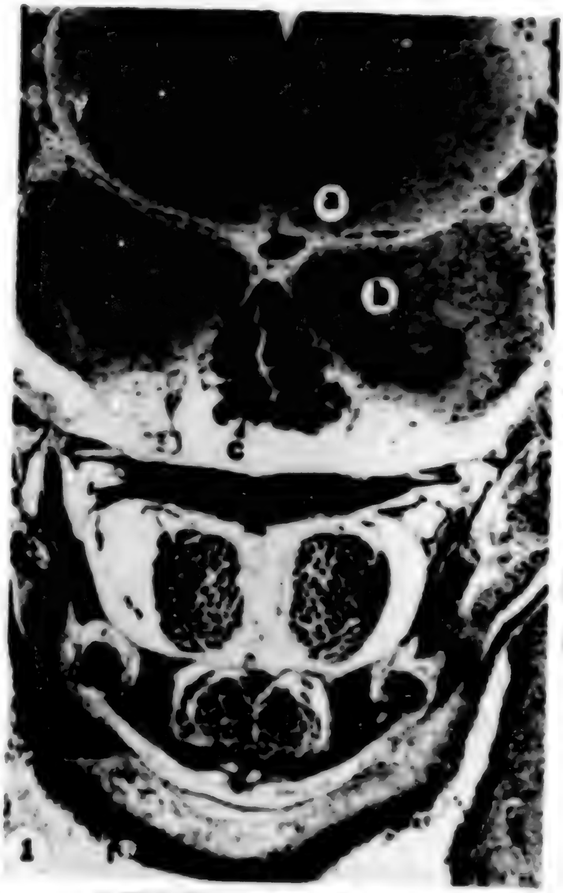
- a. Lumen of the gland
- b. Blood supply surrounding the gland

Fig. 3. Detail of portion of the saccus. × 560.

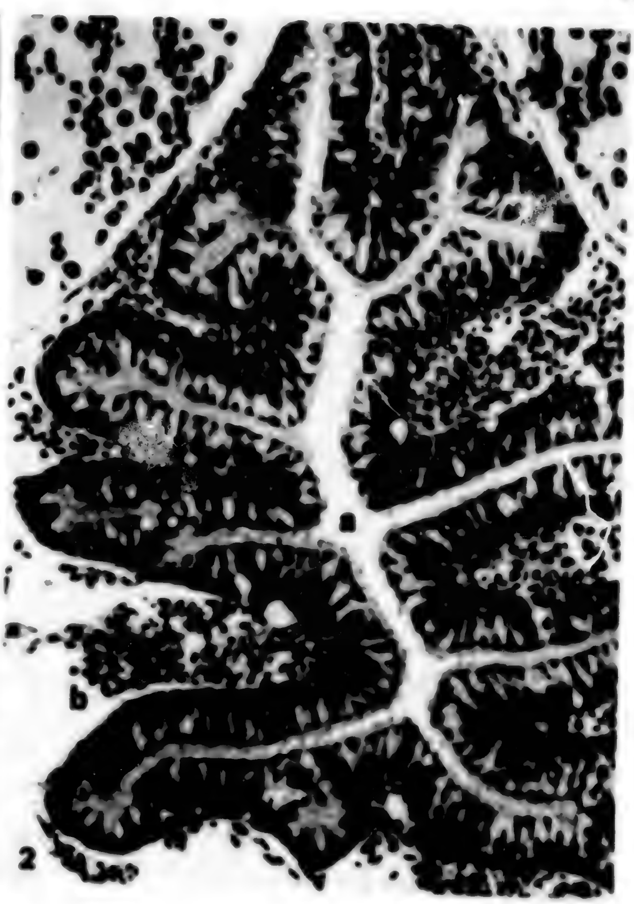
- a. Pyramidal cell nucleus
- b. Epithelial cell nucleus
- c. Blood supply

Fig. 4. Detail of fold of saccus. × 560.

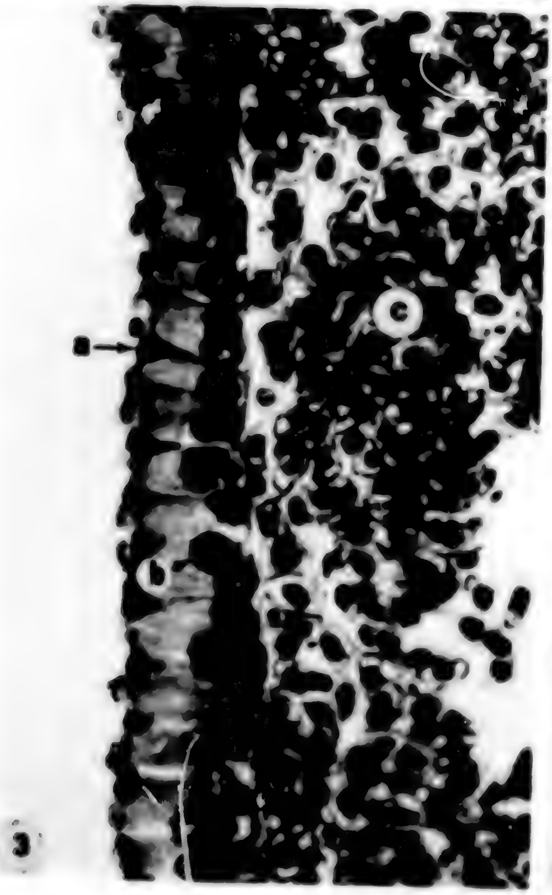
- a. Lumen of saccus
- b. Blood supply exterior to the saccus



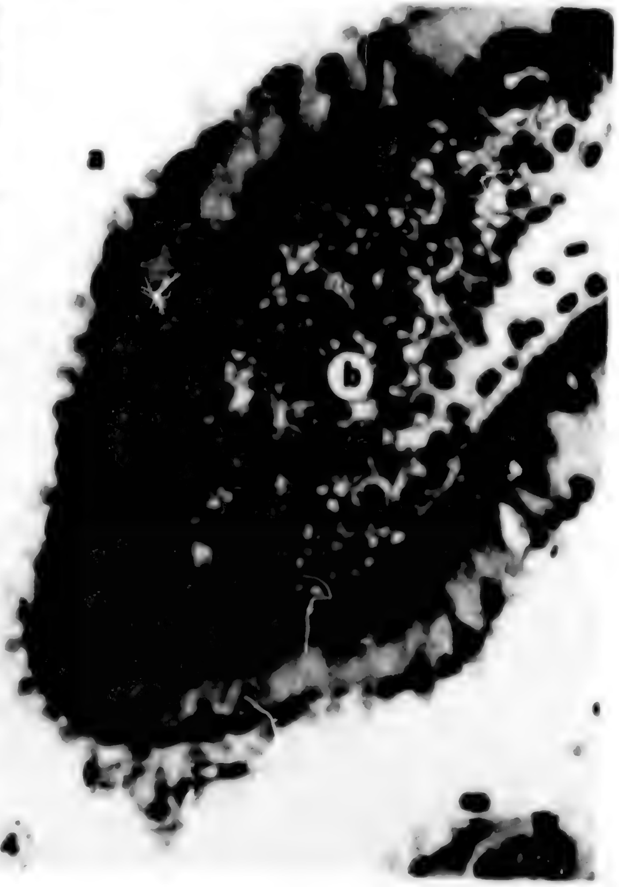
1



2



3



4

Plate 62. Ultimobranchial Gland

Fig. 1. Low power view of the ultimobranchial gland of a yearling rainbow trout. Three lobes (a) of the gland are shown in this photo. The walls of the lobes fold inward and the entire glandular mass is encapsulated by dense and loose connective tissue. × 40.

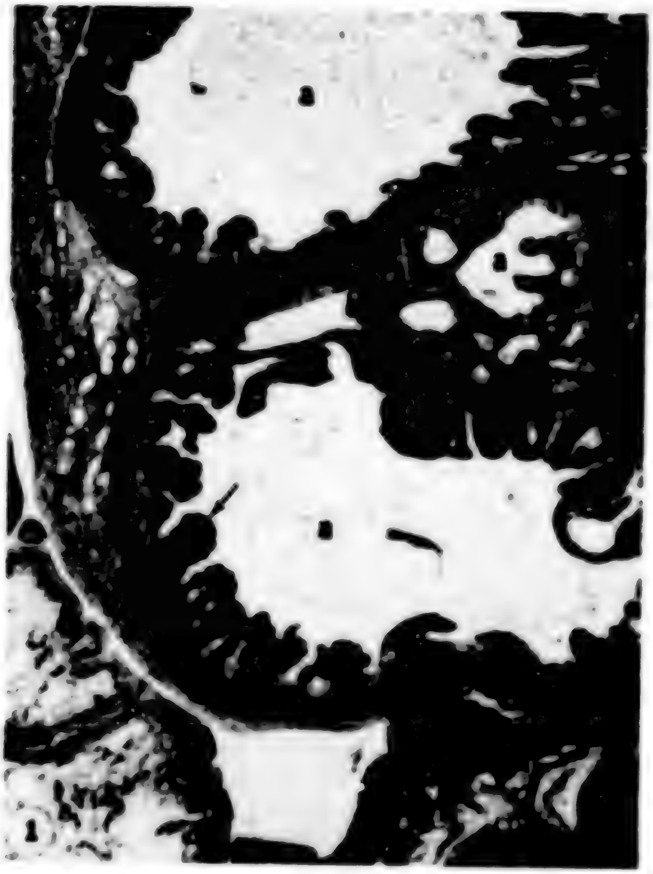
Fig. 2. Enlarged view of the folded interior of an ultimobranchial lobe. Note that the arrows in Figs. 1 and 2 point to the same fold. × 400.

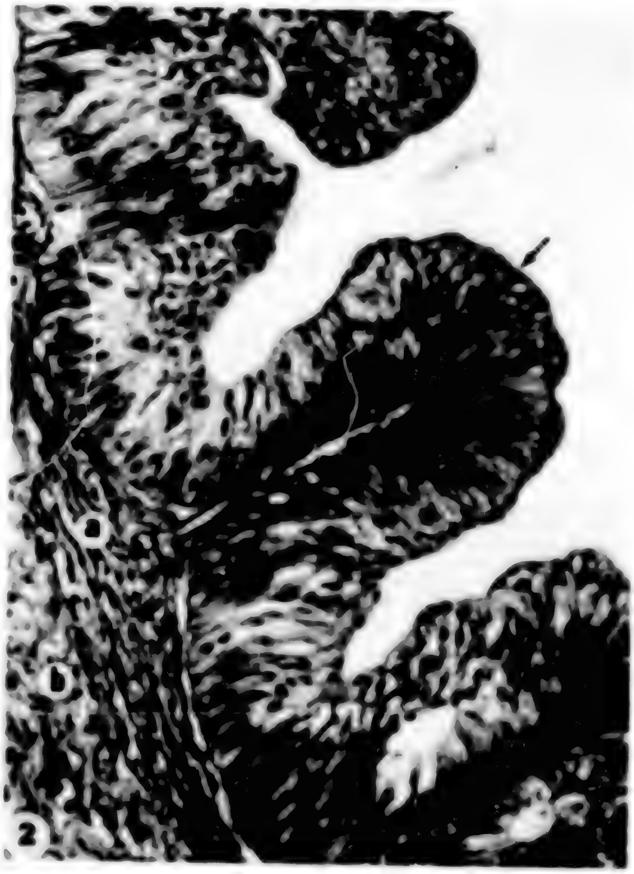
a. Dense connective tissue surrounding the gland and extending into each fold
b. Loose connective tissue exterior to the dense connective tissue capsule

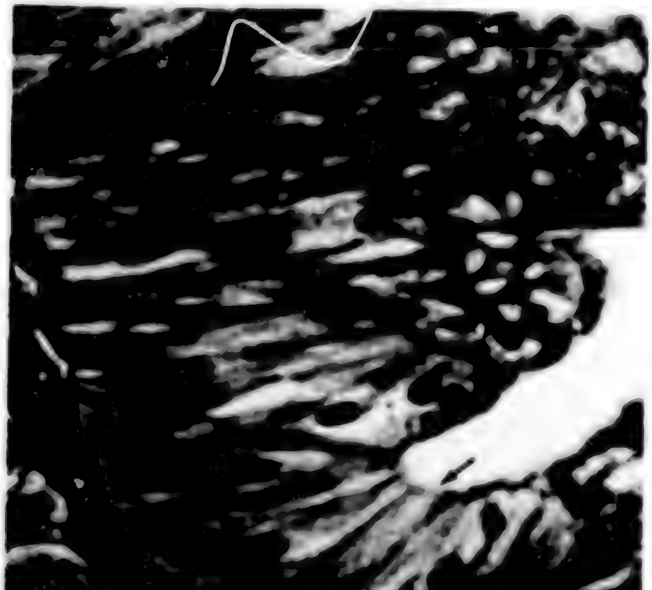
Fig. 3. Detail of the gland cells. Each cell is columnar; the apical end (arrow) discharging into the lumen, and the basal end with its elongate nucleus touching the band of dense connective tissue. × 400.

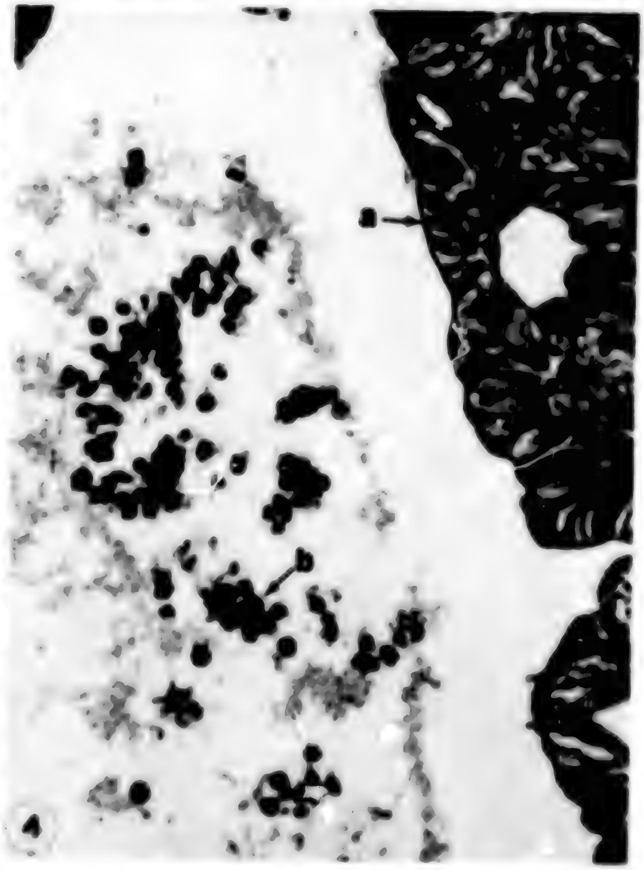
Fig. 4. Cells within the lumen of the gland. × 400.

a. Interior border of gland cells
b. Cells of unknown character within the gland lumen


a
a
a
1


a
b
2


3


a
b
4

Appendix

Fixation and Staining Procedures

Fixation Procedure of Specimens for Routine Histological or Histopathological Examination[1]

I. General Recommendations for Preparing Specimens

A. When selecting diagnostic specimens for histological examination select only fish that show the typical signs of the malady in question. The fish should be moribund (in a dying state but not dead). If possible, also include "normal" fish. If normal fish of the same species and age are not available, asymptomatic fish taken from the same group as the moribund fish will suffice.

B. Collect diagnostic specimens before any treatment of the fish is started.

C. Label all containers, showing species and date collected; distinguish between groups of fish.

D. Include a complete history
  1. Source of fish
  2. Nutrition
  3. Symptoms and date first noticed
  4. Percent mortality (daily, weekly)
  5. Water temperature
  6. Recent handling of fish
  7. Diagram of the rearing facility, showing water supply, flow, and location of affected fish
  8. List of any past diseases and their treatments (type, frequency, dosage, etc.)
  9. Any additional information that you think might be useful.

II. Fixation Procedure for Histological or Histopathological Examination

A. Select live fish only, at least five moribund and five normal fish.

B. Do not use fish that are dead or frozen or unfixed, or that have been fixed after death; they are not acceptable for histological evaluation because postmortem changes may occur in the tissue.

C. Fixation procedure
  1. The fixing solution of choice is Bouin's solution; however 10% buffered formalin is also acceptable.
  2. Kill fish by severing the spinal cord immediately posterior and dorsal to the operculum (in the nape or neck area).
  3. Slit fish ventrally from the anus to the gills.
  4. Pull viscera away from the kidney area (which is located along the backbone) and puncture the air bladder to facilitate fixation of the kidney.
  5. Slit the body muscle on either side of the dorsal fin lengthwise from behind the head to the tail. This cut is particularly important if the fish are longer than about 40 mm.
  6. Place fish or fish tissues into the fixative at volume ratio of 1:10 (fish: fixative).
  7. Leave fish tissues in the fixing solution 24–48 h and then transfer them to 70% ethyl alcohol (or leave them in the fixative if no alcohol is available).
  8. If fish are longer than 100 mm, slit intestines and kidney along entire length and open cranial cap to facilitate fixation; if they are longer than 160 mm, cut small thin pieces of each organ (i.e., gill, heart, liver, spleen, kidney, muscle, caeca, digestive tract, and any lesion observed). The pieces can be up to 25 mm square but no thicker than 5 mm.

III. Instructions for Shipping Specimens to the Laboratory

A. After the specimens have been in the fixative 24–48 h, transfer them into a plastic bag, add a small amount (about 10 cc) of 65–70% ethyl alcohol or fixative (to keep the tissue moist), and seal.

B. Bottles containing specimens may be shipped, but there is danger of breakage or leaking unless they are very well packed.

C. Box specimens in a stout container and ship by any convenient means.

---

[1] This fixation procedure was prepared by the National Fishery Research Center, U.S. Fish and Wildlife Service, Seattle, Washington.

IV. Fixatives Used for Fish Tissue

A. Bouin's Solution

Saturated picric acid

Picric acid	21 g
Distilled water	1,000 mL

Bouin's Fluid

Saturated picric acid	1,500 mL
Formalin	500 mL
Glacial acetic acid	100 mL

Solution should keep for at least 6 months if it is protected from freezing and excessive heat.

B. Bouin–Hollande Sublime

1. Stock solutions

   Solution A
   - a. Add 2.5 g cupric acetate to 100 mL distilled water
   - b. Add 4 g picric acid and stir until dissolved
   - c. Filter
   - d. Add 10 mL formaldehyde and 1 mL acetic acid to filtrate

   Solution B
   - a. Prepare saturated mercuric chloride (2 g mercuric chloride in 20 mL distilled water—approximately 10% solution)
   - b. Cool and filter
2. Working solution
   - a. Add 9 parts of Stock Solution A to 1 part of Working Solution B (fixation time 24–48 h)
   - b. Store tissues in 70% ethyl alcohol

     (This fixative is especially good for Masson trichrome stain.)

C. Buffered Neutral Formalin Solution

Formaldehyde (37–40%)	100 mL
Distilled water	900 mL
Sodium phosphate (monobasic)	4 g
Sodium phosphate (dibasic)	6.5 g

Staining Procedures

Hematoxylin and Eosin Stain

A. Stock Solutions

1. *Harris hematoxylin stock* (good for abo [illegible] months)

Hematoxylin	4 g
95% ethanol	40 g
$AlNH_4(SO_4)_2 \cdot 12H_2O$ (aluminum ammonium sulfate)	80 g
Distilled water	800 g
Mercuric oxide	2 g
Acetic Acid	20 drops

   - a. Dissolve hematoxylin in alcohol
   - b. Dissolve aluminum ammonium sulfate in distilled water and boil
   - c. Add hematoxylin solution to aluminum ammonium sulfate and boil 1/2 min
   - d. Add to mixture mercuric oxide and cool rapidly
   - e. Add acetic acid (watch to see that it turns to tomato color)

2. *Eosin Stock* (Putt's eosin)

Eosin Y (Color Index No. 45380)	10 g
Potassium dichromate	5 g
Saturated aqueous picric acid	100 mL
Absolute ethanol	100 mL
Distilled water	800 mL
Glacial acetic acid	10 drops

   - a. Mix all above except glacial acetic acid
   - b. Add glacial acetic acid
   - c. Stir until dissolved

3. *Saturated Aqueous Picric Acid*

   Picric acid

   Distilled water

   Dissolve picric acid in distilled water until a few crystals remain undissolved

B. Working solutions

1. *Harris hematoxylin* (warm and filtered)

   Should be warm enough so that it runs down a glass rod in layers when the rod is taken out of the solution. Viability of the stain can be checked by placing a few drops into a beaker of water. If it immediately turns purple or blue it is usable, but if it remains a reddish color or takes a while to change from reddish to purple, it is probably too old, and a new solution should be made.

2. *Ammonia 70% alcohol*

Ammonium hydroxide	10 drops
70% ethanol	250 mL

3. *Eosin*

Stock eosin	100 mL
Distilled water	100 mL

4. *Acid alcohol* (vary concentration if destaining is inadequate)

HCl	1 mL
70% EtOH	99 mL

C. Procedure

1. Deparaffinize	
Xylene	5 min
Xylene	3–5 min
2. Hydrate to water	
100% EtOH	5 min
100% EtOH	5 min
95% EtOH	5 min
70% EtOH	5 min
70% EtOH	5 min
Water	rinse
3. Stain	
Harris hematoxylin (warm and filtered)	15 min
Running water	rinse

BEST AVAILABLE COPY

4. Destain

Acid alcohol	3–10 quick dips (or until specimen is rose-colored; nuclei should be distinct)
Ammonia 70% alcohol	until dark blue

5. Counterstain

Eosin	15 s to 2 min (usually 3–4 dips; check under microscope for color, to prevent the stain's becoming too red)

6. Decolorize and dehydrate

70% EtOH	3 min
70% EtOH	5 min
70% EtOH	5 min

Check to see if excess eosin has been removed (less time may be required)

95% EtOH	2–3 min, depending on redness
100% EtOH	2–3 min, depending on redness
100% EtOH	3 min
Xylene	5 min
Xylene	5 min

D. Results

Nuclei – blue

Cytoplasm – various shades of pink, identifying different tissue compounds

E. Reference

Modified from G. L. Humason. 1967. Animal tissue techniques, 2nd ed. W. H. Freeman and Co. 569 pp.

II. Leishman-Giemsa Stain (for blood smears and tissue imprints)

A. Solutions

1. *Leishman Blood Stain*
2. *Giemsa Stain*

Stock

Giemsa powder	1 g
Glycerin	66 mL

Mix glycerine and Giemsa powder. Place in oven at 56–66° C for 0.5–1 h. Finally add 66 mL absolute methonol after solution has cooled.

3. *Phosphate buffer solution*, 1% (pH 6.0) (see May-Grünwald stain)
4. *Working Giemsa*

Stock Giemsa	14 mL
Phosphate buffer (6.0)	200 mL

Must be made daily.

B. Procedure

Stain slides the same day they are made. If they cannot be stained on the same day, place them in a slide box and keep them refrigerated. The slides should be stained within a few days. If deemed necessary to delay staining, double the staining time in both the Leishman and Giemsa.

Staining:

1. Fix in absolute MeOH	5 min
2. Leishman Stain	3 min
3. Working Giemsa	5 min
4. pH 6.0 phosphate buffer	Rinse well

5. Rinse in tap water to remove residual stain.
6. Air-dry overnight, and mount (if mounted immediately after staining, slide will be cloudy because drying was incomplete). Also, keep slides in the dark while they are drying, to prevent fading.

C. Reference

G. A. Wedemeyer, and W. T. Yasutake. 1977. Clinical methods for the assessment of the effects of environmental stress on fish health. U.S. Fish Wildl. Serv., Tech. Pap. 89. 18 pp.

III. Masson's Trichrome Method

A. Solutions

1. *Bouin's Solution*

(See preceding section on fixation procedure.)

2. *Weigert's Iron Hematoxylin Solution*

Solution A

Hematoxylin crystals	1 g
Alcohol, 95%	100 mL

Solution B

Ferric chloride, 29% aqueous	4 mL
Distilled water	95 mL
Hydrochloric acid, concentrated	1 mL

Working solution: Equal parts of Solution A and Solution B.

3. *Biebrich Scarlet-Acid Fuchsin Solution*

Biebrich scarlet, aqueous, 1%	90 mL
Acid fuchsin, aqueous, 1%	10 mL
Glacial acetic acid	1 mL

4. *Phosphomolybdic-Phosphotungstic Acid Solution*

Phosphomolybdic acid	5 g
Phosphotungstic acid	5 g
Distilled water	200 mL

5. *Aniline Blue Solution*

Aniline blue	2.5 g
Glacial acetic acid	2.0 g
Distilled water	100 mL

6. *2% Light Green Solution*

Light green, SF yellowish	2 g
Distilled water	98 mL
Glacial acetic acid	1 mL

7. *1% Glacial Acetic Acid Solution*

Glacial acetic acid	1 mL
Distilled water	100 mL

B. Procedure

1. Deparaffinize and hydrate to distilled water.
2. Mordant in Bouin's solution for 1 h at 56° C, or if formalin-fixed, overnight at room temperature.

3. Cool and wash in running water until yellow color disappears.
4. Rinse in distilled water.
5. Weigert's iron hematoxylin solution for 10 min. Wash in running water 10 min.
6. Rinse in distilled water.
7. Biebrich scarlet-acid fuchsin solution for 2 min. Save solution.
8. Rinse in distilled water.
9. Phosphomolybdic-phosphotungstic acid solution for 10 to 15 min before aniline blue solution. (Aqueous phosphotungstic acid 5% for 15 min before light green counterstain.) Discard solution.
10. Aniline blue solution for 5 min or light green solution for 1 min (for central nervous system 15 to 20 min). Save solution.
11. Rinse in distilled water.
12. Glacial acetic solution for 3 to 5 min. Discard solution.
13. Dehydrate in 95% alcohol absolute alcohol, and clear in xylene, two changes each.
14. Mount.

D. Results

Nuclei – black

Cytoplasm, keratin, muscle fibers and intercellular fibers – red

Collagen – blue

Note: To insure proper mordanting, Bouin's solution should be preheated to 58–60° C.

E. Reference

Modified from P. J. Masson. 1929. Trichrome stainings and their preliminary technique. J. Tech. Methods 12: 75–90.

IV. May-Grünwald Giemsa Stain (for paraffin sections)

A. Stock Solutions

1. *Jenner's Stock* (keep refrigerated)

Jenner stain	2.5 g
Methyl alcohol	1,000 mL

2. *Giemsa* (keep refrigerated)

Giemsa	3.5 g
Glycerin	231 mL
Absolute methyl alcohol	231 mL

   a. Mix glycerin and Giemsa
   b. Place in oven at 60° C for 1-1.5 h
   c. Stir often while in oven
   d. Remove from oven and add methyl alcohol
   e. Store in refrigerator (4° C)

   Note: Commercially prepared stock Giemsa can be used instead.

3. *Phosphate Buffer – pH 6.0* (keep refrigerated)

Sodium phosphate monobasic	35 g
Sodium phosphate dibasic	4.84 g
Distilled water	3,960 mL

B. Working Solutions

1. *Working Jenner Solution* (replace each week)

Stock Jenner	125 mL
Distilled water	125 mL

2. *Working Giemsa Solution* (replace each day)

Stock Giemsa	14 mL
Phosphate buffer	200 mL

3. *1% Acetic Acid*

Acetic acid, glacial	10 mL
Distilled water	990 mL

C. Procedure

1. Xylene (2 changes)	5 min each
2. 100% EtOH	4–5 dips
3. 100% EtOH	4–5 dips
4. 100% EtOH	5 min
5. 100% EtOH	5 min
6. 95% EtOH	4–5 dips
7. 95% EtOH	5 min
8. Running tap water	5 min
9. Methyl alcohol (2 changes)	3 min each
10. Working Jenner solution (replace each week)	6 min
11. Working Giemsa solution (replace each day)	overnight
12. Running tap water	4–5 dips
13. 1% acetic acid	1 quick dip
14. Running tap water	4–5 dips
15. Dehydrate (differentiate as desired while the slides are in the 95% EtOh): 3–95%; 3–100% EtOh	4–10 dips
16. Xylene (5 changes)	2 min each
17. Mount	

E. Results

Nuclei – blue

Cytoplasm – pink to rose

Bacteria – blue

F. Reference

Modified from L. G. Luna, editor. 1968. Manual of histologic staining methods of the Armed Forces Institute of Pathology, 4th edition. McGraw-Hill, New York.

V. Peroxidase Stain (for blood smear and tissue imprints)

A. Solutions

1. *Copper sulphate solution*, 1% (fixative)
2. *Benzidine solution*, 0.1% (primary stain reactant)

Benzidine	0.2 g
Distilled water	200 mL
Hydrogen peroxide (3% solution)	few drops

Dissolve benzidine with a few drops of distilled water, then add rest of water and filter. Add a few drops of 3% hydrogen peroxide, mix, and warm to 30–40° C.

3. *Safranin*, 1% solution (counterstain)

B. Procedure

For air-dried blood smears and imprints:

1. Flood slide with $CuSO_4$ solution
2. Follow immediately with Benzidine solution (a blue precipitate will form)
3. After 1 min, wash off with water and counterstain 2 min with safranin

C. Results

Granulocyte cytoplasm granules – blue
Remaining cells – red

D. Reference

Modifed from R. Yuki. 1957. Blood cell constituents in fish. I. Peroxidase staining of the leucocytes in rainbow trout (*Salmo irideus*). Bull. Fac. Fish., Hokkaido Univ. 8: 36–44.

VI. Periodic Acid Schiff (PAS)-Orange G-Light Green Stain

A. Solutions

1. *Aqueous periodic acid* – 0.5%
2. *Schiff's reagent*
   Dissolve 1 g of basic fuchsin in 200 mL of boiling distilled water. Shake for 5 min and cool to 50° C. Filter and add to the filtrate 20 mL of N-HCl. Cool to 25° C and add 1 g of anhydrous sodium (or potassium) metabisulphite ($Na_2S_2O_5$). Set this solution in the dark for 48 h – solution will become straw-colored. Store the filtrate in a dark bottle at 0–4° C. Allow it to reach room temperature before use.
3. *Aqueous Orange G*, 1%
4. *Phosphotungstic acid*, 5%
5. *Aqueous light green*, 1%

B. Procedure

1. Bring sections to distilled water
2. Oxidize in 0.5% aqueous periodic acid for 5 min
3. Treat with Schiff's reagent for 15 min
4. Wash in running water for 10 min
5. Stain in 1% aqueous orange G for 10–15 s
6. Mordant in 5% phosphotungstic acid for 15 s
7. Rinse in running tap water for 15 s
8. Stain in 1% aqueous light green for 1 min
9. Rinse briefly in 1% acetic acid
10. Dehydrate in alcohols, clear and mount

C. Results

Somatotropin cells – Orange G positive
Thyroid stimulating hormone and growth hormone cells – PAS positive
ACTH cells – light green positive
Prolactin cells – PAS negative

D. Reference

Modified from A.G.E. Pearce. 1961. Pages 821–823 *in* Histochemistry – theoretical and applied. Little, Brown and Co., Boston.

Index[1]

Abductor muscle, gill, 62
A-cells, pancreatic, 27, *58*
Acellular bone, 7
Acini, pancreatic, 26, *56*, *57*, *58*, *78*
Adductor muscle, gill, 62
Adenohypophysis, 152, *160*, *162*
Adipose tissue, 26, *44*, *56*, *78*, 134
Adrenal tissue, 153, *168*, *170*
Adrenal cortical tissue (*see* Interrenal tissue)
Adrenocorticotrophic cells, 153, *162*, *164*
Adventitia, 71
Afferent artery
  gill, *62*, *66*, *74*
  pseudobranch, *68*
Agranular cells, corpuscles of Stannius, 154
Air bladder (*see* Swim bladder)
Alpha cells (*see* A-cells)
Ameloblasts (*see* Inner enamel epithelium)
Anal papilla, *50*
Anus (*see* Vent)
Aorta, 71, *74*, *166*
Arteries, 71, *74*, *78*
Arteriole
  afferent glomerular, 97, *100*
  efferent glomerular, 97, *100*
  in liver, *52*, *78*
  in pancreas, *56*, *78*
Astrocytes, 104
Atrio-ventricular valve, *32*, 70
Atrium, *6*, 70, *75*, *76*
Auditory tissue, 118, *138*
Auerbach's plexus, *44*, *56*
Axon, 104

Basement membrane, *42*, *44*, 97, *100*
Basihyal cartilage, *34*
Basibranchium, *130*
B-cells, pancreatic, 27, *58*
Beta-cells (*see* B-cells)
Between brain (*see* Diencephalon)
Bile duct, 26, *52*, *54*, *78*
Biliary tissue, *24*, 26, *54*
Blast cells, blood (*see* Stem cells)
Blood
  cells, 82–83, *87*, *88*
  stains, 182
Bone, 7, *10*
Bouin's fluid (*see* Fixatives)
Bouin-Hollande fluid (*see* Fixatives)
Bowman's
  capsule, kidney, 97, *100*
  membrane, eye, *124*
Brain, *3*, *4*, *6*, 104, *108*, *110*
Brockman bodies (*see* Islet of Langerhans)
Brush border (*see* Striated border)
Buccal cavity (*see* Oral cavity)
Bulbus arteriosus, *6*, *32*, 70, *75*, *76*

Calcitonin, 154
Cardiac glands, 25, *36*, *38*
Cardiac muscle, 8, *76*
Cardiac stomach, 25, *36*, *38*
Cardinal vein, posterior (*see* Posterior cardinal vein)
Cardiovascular system, 70–71, *74–81*
Carotenoid granules, 14
Cartilage, *4*, 7, *10*, *34*
Caudal neurosecretory tissue, 105, *114*
Caudal pars distalis (*see* Proximal pars distalis)
Cellular bone, 7
Central nervous system, 104–105, *108–115*
Central vein, liver, 26, *52*
Cerebellar valvula, *3*, *32*
Cerebellum, *3*, *4*, *32*, *108*
Cerebral hemisphere, *6*
Chemosensory cells, 14
Chloride cells
  epidermis, 14
  gill, 62, *66*
Chondroblasts, 7
Chondrocytes, 7, *66*
Chondroid-like cells, *10*
Choroid, 27, 62, *124*
Chromaffin tissue, 153–154, *168*, *170*
Chromatophores, 14–15, *22*
Circulatory system (*see* Cardiovascular system)
Club cells, 14
Collecting duct, kidney, 97, *102*
Collagen, 14
Common cardinal vein, 70, *81*
Cones, retina, 117, *124*, *126*
Connective tissue
  fibrous, 7, 27, *60*
  loose, *134*
  reticular, *92*
Cords, liver, 26, *52*
Cornea, *124*
Coronary artery, *75*
Coronet cells, 154
Corpuscles of Stannius, 154, *172*, *174*
Cortical steroid, 153
Corticotrophs (*see* Adrenocorticotrophic cells)
Ctenoid scales, 14
Cupula, 118, *134*, *136*
Cycloid scales, 14

Dahlgren cells, 105, *114*

---

[1] Illustrative materials are indicated by italicized numbers.

D-cells, pancreatic, 27
Dendrites, 104, 117
Dentary cartilage, *34*
Dentine, 24, *34*
Depressor dorsalis, *12*
Dermis, *12*, 14–15, *22*, *47*
Descemet's endothelium, *124*
Descemet's membrane, *124*
Diencephalon, *3*, *32*, *108*, *162*, 192
Digestive system, 24–27, *32–51*
Distal tubule, kidney, 98, *100*, *102*
Dorsal aorta, *10*, *74*
Dorsal aorta ligament, *10*, 71
Dorsal fin, *12*
Dorsalis
  depressor, *12*
  erector, *12*
Drosopterin granules, 14
Ducts of Cuvier (*see* Common cardinal vein)
Dura mater, 104, *110*

Efferent artery, gill, *62*, *66*, *74*
Elastic cartilage, 7
Elastic connective tissue, 71, *76*
Enamel, 24, *34*
Enameloid, 24
Endocardium, 70
Endocrine system, 152–154, *160–179*
Endocrine tissue, 26–27, 152–154, *160–179*
Endolymph, 118
Endomysium, *12*
Ependymal cells, 104
Epicardium, 70, 75
Epidermis, *4*, *12*, *14*, *15*, *18*, *20*, *22*
Epinephrine, 153
Epithelium
  columnar, *40*, *48*, 97–98
  corneal, *124*
  outer enamel, *34*
  sensory, olfactory, *128*
  squamous, *66*, *100*
  stratified squamous, *132*
Erector dorsalis, *12*
Erythroblast, *88*
Erythrocytes, 82, *87*, *88*
Esophageal gland, 25, *36*
Esophageal mucosa, crypt of, *36*
Esophagus, *23*, 25, 26, *36*, *130*
Exocrine tissue, 27
Eye, 117, *124*, *126*

Fat cells (*see* Adipose tissue)
Fiberblasts, 14
Fibrocyte, *12*
Fibrous cartilage, 7
Fibrous connective tissue, 7
Fixation procedures, 180
Fixatives
  Bouin's fluid, 1, 181
  Bouin-Hollande Sublime, 181
  Buffered neutral formal solution, 181
Follicle
  ovarian, *52*, *150*
  thyroid, *166*
Forebrain (*see* Telencephalon)

Gall bladder (*see* Biliary tissue)
Ganglion, *4*, *108*, *112*
Ganglion cell layer, retina, 117, *126*
Gas bladder (*see* Swim bladder)
Gastric pit, 25
Ghost cells (*see* Smudge cells)
Gill
  arch, *3*, *6*, 62, *68*, *94*
  lamellae, *3*, 62, *66*
  filaments, *3*, 62, *66*
Glomerulus, 97, *100*
Glucagon, 27
Goblet cells (*see* Mucous cells)
Gonadotropin, 153
Granular cells
  digestive tract, 25, *38*, *42*
  epidermis, 14
  gill, 82
  stomach, *38*, *42*
  corpuscles of Stannius, 154
Granular layer, optic tectum (*see* Stratum periventriculare)
Granulocytes, 82, *88*
Gray matter, *108*, *110*
Ground substance, 14
Growth hormone (*see* Somatotropin)
Guanine, 14, *22*
Gustatory tissue, 24, 117–118, *130*
Hassel's corpuscles, 91
Head kidney, *6*, *32*, *88*, 91
Heart, *6*, 70–71, *74*, *75*
Hemal vein, 10
Hematopoietic tissues
  kidney, *32*, *88*, 91, *100*, *170*, *172*
  spleen, 91, *92*
  thymus, 91, *94*
Hemocytoblast, *88*
Hepatic
  artery, 26
  sinusoid, 26, *52*
  vein, 27
Hepatic portal
  system, 26
  triad, *78*
Histocytes, 83
Holocrine gland, 14
Hyaline cartilage, 7, *10*
Hyomandibular canal, *134*
Hypodermis, 15
Hypophysis (*see* Pituitary)
Hypoxanthine (*see* Guanine)

Infectious hematopoietic necrosis, 25, 82
Infundibulum, 152, *160*, *162*
Inner enamel epithelium, *34*
Inner nuclear layer, retina, 117, *126*
Inner plexiform layer, retina, 117, *126*

Insulin, 27
Intercellular substance, 14
Interrenal tissue, 153, *168*, *170*
Intestine
  ascending, 25, *46*
  descending, 25, *50*
Intima
  arteries, 71
  veins, 71
Involuntary muscle (*see* Smooth muscle)
Iridophores, 14, *15*, *22*
Iris, *124*
Islet of Langerhans, 27, *56*, *58*

Juxtaglomerular cells, 97

Keratinocytes, 14
Kidney, *10*, 91, 97–99, *100–102*
  (*see also* Hematopoietic kidney and urinary system)
Kupffer cells, *52*
Lagena, 118
Lamina epithelialis, *40*, *54*, *60*, *82*, *88*
Lamina propria
  gall bladder, *54*
  intestine, *46*, *48*
  pyloric caeca, *44*
  stomach, 25, 38, *40*, *42*
Lamellae
  gill (*see* Gill, lamellae)
  ovary (*see* Ovigerous lamellae)
Lateral line tissue, 118, *134*, 136
Leishman-Giemsa stain, 182
Lens, 117, *124*
Ligament, interior longitudinal, *10*
Liver, *6*, 25–26, 38, *52*
Lymph
  heart valve, 71
  vessel, *134*, *136*
Lymphatic system, 71, *80*
Lymphocyte
  cells, 82, *87*, *88*
  wandering, 25, *44*, 98, *128*

Macrophages, 83, 91
Macula, *138*
Malpighian cells, 14
Masson's trichrome stain, 182
Mauthner cells, 104–105, *110*
Media
  arteries, 71
  veins, 71
Medulla oblongata, *3*, *6*, *32*, *108*
Melanin-macrophage centers, 91
Melanophores, 14, *15*, *22*, 91, *100*, *174*
Mesangial cells of glomerulus, 97
Mesencephalon (*see* Optic lobe)
Mesenchymal tissue, *3*, *4*, *108*
Mesoadenohypophysis (*see* Proximal pars distalis)
Mesonephric duct, 97, *102*
Mesorchium, 145
Mesovarian mesentery, 145

Metaadenohypophysis (*see* Pars intermedia)
Metencephalon (*see* Cerebellum)
Microridges, epidermis, 14, *18*
Molecular layer, optic tectum (*see* Stratum marginale)
Monocytes, 83
Mucosa
  esophagus, 25, *36*
  stomach, 25, *38*
  intestine, 25
Mucous cells
  digestive tract, 25, *46*, *142*
  epidermis, *12*, 14, *20*, *134*
  gill, 70, *66*
  olfactory epithelium, 117, *128*
Muscle, *4*, 7–8, *10*, *12*, *18*, *20*
Muscularis
  digestive tract, 25, *36–51*
  gall bladder, 2, *54*
  swim bladder, 27, *60*
Myelencephalon (*see* Medulla oblongata)
Myelinated nerve fiber (*see* White matter)
Myocardium, 70
Myofibrils, 7
Myofilaments, 7
Myomere, *12*
Myosepta, *12*

Nephrons, types of, 97
Nerve cell layer, retina, 117, *126*
Nervous system, 104–107, *108–115*
Neuroglial cells, 104, 105, *110*, *114*
Neurohypophysis, 152, *160*, *162*
Neurolemma, 105, *112*
Neurons, 104, 105
Neurophil, 104
Neuromasts
  tactile organ, 117, *132*
  lateral line, 118, *134*
Neurosecretory system, 105, *114*
Neurosensory cells, olfactory epithelium, 117
Neutrophils, 82–83, *87*, *88*
Noreinepinephrine, 153
Notochord, 7, *10*, *32*, *108*
Nuclear shadow (*see* Smudge cells)

Odontoblasts, *34*
Olfactory tissue, *3*, 117, *128*
Oligodendrocytes, 104
Oocytes, 145, *150*
Oogonia, 145
Operculum, *4*, *68*
Optic lobe, *3*, *4*, *110*, *108*, 117
Optic nerve, *3*, *112*, *124*
Optic tectum (*see* Optic lobe)
Oral cavity, *3*, *24*, *34*
Oral valve, *3*, *34*
Outer nuclear layer, retina, 117, *126*
Outer plexiform layer, retina, 117, *126*
Osmoregulation, 154
Osteoblasts, 7
Osteocytes, 7

Otolith, *138*
Ovigerous lamellae, *150*
Ovary, 145, *150*

Papillae (*see* Taste buds)
Pancreas, 27, *56*, *58*, *78*
Pancreatic duct, *58*
Parasympathetic ganglion cell (*see* Auerbach's plexus)
Pars intermedia, 152–153, *160*, *162*
Pericardium, 70
Peroxidase stain, 183
Pharynx, *3*, 24, *32*, *130*
Pia mater, 104, *110*
Pigment cells, 14–15, *22*
Pilaster cells, *62*, *66*, *68*
Pillar cells (*see* Pilaster cells)
Pineal organ, *3*, 118–119, *140*
Pituitary, *32*, 152–153, *160*, *162*, 164
Pneumatic duct, *32*, *36*
Podocytes, Bowman's capsule, 97, *100*
Polychromatocyte, 82, *87*, *88*
Polymorphonuclear leukocytes (*see* Neutrophils)
Postcardinal vein (*see* Posterior cardinal vein)
Posterior cardinal vein, *10*, 153, *168*, *170*
Primordial germ cells, 145
Proadenohypophysis (*see* Rostral pars distalis)
Prolactin cells, 152, *162*, *164*
Prolymphocyte, *88*
Proximal pars distalis, 152–153, *162*, *164*
Proximal segment, renal tubule, 97–98, *100*, *102*
Pseudocartilage, 7
Pseudobranchs, *62*, *68*
Pulp, tooth, *34*
Purkinje cells, 104, *110*
Pyloric caeca, *6*, 24, 25, *44*, *56*
Pyloric stomach, *6*, 25, *40*, *41*

Rectum, *3*, 24, 25, *50*
Receptor cells, lateral line, *136*, *138*
Red muscle, 8
Red pulp, spleen, 91, *92*
Renal corpuscle, 97
Renal tubules, 97–98, *100*, *102*
Reproductive system, 145–147, *148*, *150*
Respiratory system, 62–65, *66*, *68*
Rete mirabile, 27
Reticular cells, thymus, *94*
Retina, *4*, 117, *124*, *126*
Rodlet cells, 119, *142*
Rods, retina, 117, *124*, *126*
Rostral pars distalis, 152–153, *160*, *162*, *164*

Sacculus, 118, *138*
Saccus dorsalis, *140*
Saccus vasculosus, *3*, *32*, 154, *160*, *176*
Sagitta, *138*
Scales, 14, *18*, *20*
Schwann cell (*see* Neurolemma)
Semicircular canals, *4*, 118, *138*
Sensory cells
  lateral line, 118, *134*, *136*
  pineal organ, *140*
Sensory papilla, tactile, *132*
Serosa
  esophagus, 25
  gall bladder, *54*
  intestine, 25, *44*, *48*
  stomach, 25, *40*, *42*
  swim bladder, 27, *60*
Serous cardiac glands, 25, *36*
Sinus venosus, 70
Skin, 14, *18*, *20*
Sino-atrial valve, *32*, 70, *75*
Sinusoid
  liver, 26, *52*, *78*
  kidney, *102*
Skeletal muscles (*see* Striated muscles)
Smooth-celled cartilage, 7
Smooth muscle, 7–8, 70, 71, 98, *102*
Smudge cells, 82, *87*
Somatotropin, 153, *162*, *165*
Special sensory organs and tissues, 117–123, *124–143*
Spermatids, 145, *148*
Spermatocytes, 145, *148*
Spermatogenesis, 145, *148*
Spermatogonia, 145
Spermatozoa, 145, *148*
Spinal cord, *10*, *32*, 105, *108*
Spleen, *6*, *24*, 91, *92*
Staining procedures
  hematoxylin and eosin stain, 181–182
  Leishman-Giemsa stain, 182
  Masson's trichrome method, 182–183
  May-Grünwald-Giemsa stain, 183
  peroxidase stain, 183–184
  periodic acid Schiff (PAS)-Orange G-light green stain, 184
Stem cell, blood, *88*, 91
Stomach
  cardiac region, *6*, 25, *38*
  pyloric region, *6*, 25, *40*, *42*
Stratum album centrale, 104, *110*
Stratum compactum
  esophagus, 25
  gall bladder, *54*
  intestine, *46*, *48*, *50*
  pyloric caeca, *44*
  skin, 14, *20*, *134*
  stomach, 25, *38*, *42*
Stratum fibrosum et griseum superficiale, 104, *110*
Stratum fibrosum marginale, 104, *110*
Stratum granulosum
  esophagus, 25
  externum, 25
  internum, 25
  intestine, *46*, *48*
  stomach, 25, *38*, *42*
Stratum griseum centrale, 104, *110*
Stratum opticum, 104, *110*
Stratum periventriculare, 104, *110*
Stratum spongiosum, 14, *20*, *134*
Striated border, *44*, *48*, 97, *100*
Striated muscles
  body musculature, 7, *10*, *12*, *18*, *20*
  heart, 8, *76*

Subarachnoid space, *110*
Subcutis, 15
Submucosa
  esophagus, 25, *36*
  stomach, 25, *40*
Subocular lymphatic sac, *80*
Supportive tissues, 7-9, *10-13*
Swim bladder, *6*, *24*, 27, *60*
Synapses, nervous tissue, 104

Tactile organs (*see* Neuromasts)
Taste buds (*see* Gustatory tissue)
Teeth, *3*, 24, *34*
Telencephalon, *3*, *4*, *32*, 108
Tenth cranial nerve (*see* Vagus nerve)
Testes, 145, *148*
Theca, *150*
Thrombocytes, 83, *87*
Thymic bodies, 91, *94*
Thymocytes, *94*
Thymus, *4*, 91, *94*, *138*
Thyroid, *78*, 153, *166*
Thyroid stimulating hormone (*see* Thyrotropin)
Thyrotropin, 153, *164*
Thyroxine, 153
Tongue, *3*
Trabecular, heart, 70
Transitional region, stomach, 25
Transverse septum, 26, *52*
Tunica albuginea, 145

Ultimobranchial gland, 154, *178*
Urophysis (*see* Caudal neurosecretory tissue)
Urinary
  bladder, *6*, *24*, 97
  duct, 97
  system, 97-99, *100-103*
Urogenital papillae, 97
Utriculus, 118

Vacuoles
  fat (*see* Adipose tissue)
  glycogen, *52*
Vagus nerve, *108*, *112*
van Kupffer cells (*see* Kupffer cells)
Vein, 71, *78*, *79*, *92*
Vent, 24, *50*
Ventral aorta, 71, *78*
Ventricle
  brain, *3*, *32*, *108*
  heart, *6*, 22, *52*, 70-71, *74*
Venules, 26, *78*
Ventriculo-bulbar valve, *32*
Ventebral column, *6*
Vertebra, *10*
Villi, intestine, *92*
Voluntary muscle (*see* Striated muscle)
Vomer cartilage, *34*
Vomerine tooth, *34*

White matter, *108*, *110*
White muscle, 8
White pulp, spleen, 91, *92*

Xanthophores, 14, *15*, *22*
X-cells, 27

Yolk, *150*

Zona radiata, *150*
Zymogen granules, pancreas, 26, *56*, *58*

A list of current *Resource Publications* follows.

133. A Handbook for Terrestrial Habitat Evaluation in Central Missouri, edited and compiled by Thomas S. Baskett, Deretha A. Darrow, Diana L. Hallett, Michael J. Armbruster, Jonathan A. Ellis, Bettina Flood Sparrowe, and Paul A. Korte. 1980. 155 pp.
134. Conservation of the Amphibia of the United States: A Review, by R. Bruce Bury, C. Kenneth Dodd, Jr., and Gary M. Fellers. 1980. 34 pp.
135. Annotated Bibliography for Aquatic Resource Management of the Upper Colorado River Ecosystem, by Richard S. Wydoski, Kim Gilbert, Karl Seethaler, Charles W. McAda, and Joy A. Wydoski. 1980. 186 pp.
136. Blackbirds and Corn in Ohio, by Richard A. Dolbeer. 1980. 18 pp.
137. Handbook of Acute Toxicity of Chemicals to Fish and Aquatic Invertebrates, by Waynon W. Johnson and Mack T. Finley. 1980. 98 pp.
138. Waterfowl and their Wintering Grounds in Mexico, 1937-64, by George B. Saunders and Dorothy Chapman Saunders. 1981. 151 pp.
139. Native Names of Mexican Birds, researched and compiled by Lillian R. Birkenstein and Roy E. Tomlinson. 1981. 159 pp.
140. Procedures for the Use of Aircraft in Wildlife Biotelemetry Studies, by David S. Gilmer, Lewis M. Cowardin, Renee L. Duval, Larry M. Mechlin, Charles W. Shaiffer, and V. B. Kuechle. 1981. 19 pp.
141. Use of Wetland Habitats by Birds in the National Petroleum Reserve—Alaska, by Dirk V. Derksen, Thomas C. Rothe, and William D. Eldridge. 1981. 27 pp.
142. Key to Trematodes Reported in Waterfowl, by Malcolm E. McDonald. 1981. 156 pp.
143. House Bat Management, by Arthur M. Greenhall. 1982. 30 pp.
144. Avian Use of Sheyenne Lake and Associated Habitats in Central North Dakota, by Craig A. Faanes. 1982. 24 pp.
145. Wolf Depredation on Livestock in Minnesota, by Steven H. Fritts. 1982. 11 pp.
146. Effects of the 1976 Seney National Wildlife Refuge Wildfire on Wildlife and Wildlife Habitats, compiled by Stanley H. Anderson. 1982. 28 pp.
147. Population Ecology of the Mallard. VII. Distribution and Derivation of the Harvest, by Robert E. Munro and Charles F. Kimball. 1982. 126 pp.
148. Management of Seasonally Flooded Impoundments for Wildlife, by Leigh H. Fredrickson and T. Scott Taylor. 1982. 29 pp.
149. Mitigation and Enhancement Techniques for the Upper Mississippi River System and Other Large River Systems, by Rosalie A. Schnick, John M. Morton, Jeffrey C. Mochalski, and Jonathan T. Beall. 1982. 714 pp.

END

11-15-83